Anatomy of a Late Triassic Bristol fissure: Tytherington fissure 2

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A R T I C L E   I N F O

A B S T R A C T

The Late Triassic and Early Jurassic fissures around Bristol and South Wales are famous as sources of excellent fossils of early mammals, dinosaurs, sphenodontians, and other tetrapods. However, the ways in which these fissures filled with sediment have not often been documented. Moreover, systematic faunal sampling up a working face exposure has rarely been attempted for the UK Triassic fissures. Here we show in detail how a complex fissure in Tytherington Quarry, north-east of Bristol, filled in multiple steps, and document both sedimentary facies and faunas. Tytherington Quarry is a key Late Triassic Bristol sauropsid fissure site, having previously yielded abundant *Thecodontosaurus* remains and a new genus of sphenodontian, *Diphydontosaurus*. Our findings comprise specimens of terrestrial reptiles, including sphenodontians and archosaurs. However, abundant remains of fishes and marine invertebrates were also recovered, indicating a significant marine influence during parts of the fissure-filling process. Comparisons of our results with those of previous studies on Tytherington and other Late Triassic SW UK fissure sites indicate some consistent patterns of faunal association and provide further evidence of a Rhaetian age for the Late Triassic palaeo-island fissures north of Bristol. Our analysis supports a model of fissure formation and filling entailing punctuated episodes of sedimentation through a relatively short time.

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1. Introduction

The close of the Triassic was a time of widespread palaeogeographical and environmental change. At the beginning of the Rhaetian stage (duration 4.1 Myr; 205.5–201.4 Ma; Kent et al., 2017), the breakup of Pangaea initiated the Rhaetian Transgression, a Europe-wide event entailing the flooding of continental red-bed environments by epicontinental seas (Fischer et al., 2012; Suan et al., 2012). In the area around Bristol and the Severn Estuary, Rhaetian sediments, all components of the Penarth Group, rest horizontally either conformably on underlying units of the Mercia Mudstone Group such as the Blue Anchor Formation, or unconformably on an uplifted and eroded Carboniferous Limestone landscape (Robinson, 1957; Savage, 1993; Benton and Spencer, 1995; Whiteside and Marshall, 2008; Whiteside et al., 2016). Here and there, the Carboniferous limestones formed palaeo-highs characterized by karstic features (Robinson, 1957) including fissures, of which the Tytherington fissures are an example (Whiteside and Marshall, 2008; Whiteside et al., 2016). These outcrops were part of a small

sub-tropical archipelago (Fig. 1A) swept by episodic rains (Whiteside and Robinson, 1983) that washed lateritic soils into the fissures. The sediments often contain the remains of insular animals, such as the dinosaur *Thecodontosaurus*, other archosaurs, and abundant sphenodontians. This assemblage, dominated by terrestrial reptiles, was designated the 'sauropsid' fauna by Robinson (1957) to distinguish it from fissure deposits containing plentiful mammals, of Early Jurassic age (Robinson, 1957; Whiteside and Marshall, 2008; Whiteside et al., 2016).

The chronostratigraphic and palaeoenvironmental contexts of the Bristol sauropsid fissures (Cromhall, Durdham Down, Tytherington and Woodleaze) have been the subject of longstanding debate (Walkden and Fraser, 1993; Simms et al., 1994; Whiteside and Marshall, 2008; Whiteside et al., 2016). Fossils in all the sauropsid fissure deposits, including those at Tytherington, have been documented from sediments processed in the laboratory (Whiteside, 1983; Whiteside and Marshall, 2008; van den Berg et al., 2012; Whiteside et al., 2016). Although Whiteside and Marshall (2008, fig. 17) made a systematic count of sphenodontian taxa in all the Tytherington fissures, and van den Berg et al. (2012) presented a comprehensive faunal analysis of an exposure of Fissure 2, only at Cromhall Quarry have detailed attempts been made to match sedimentology and fossil faunas with Late Triassic
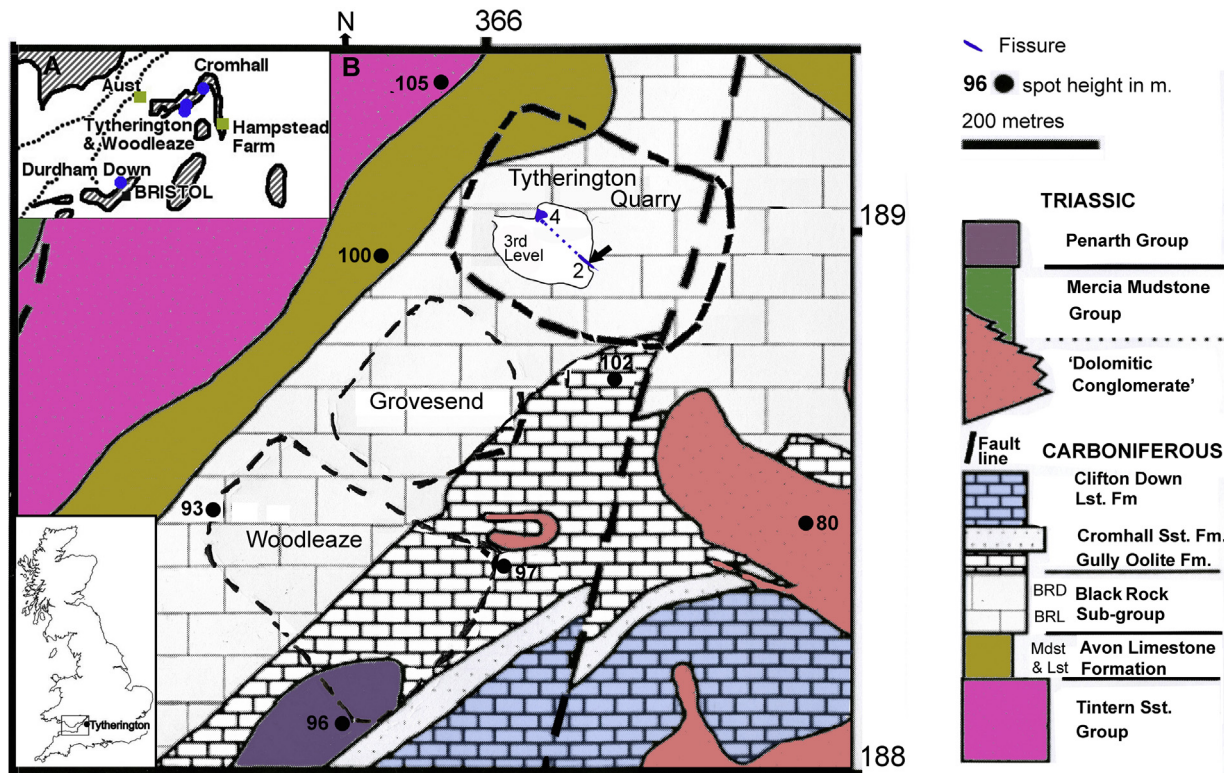
Fig. 1. Palaeogeography of the Bristol Channel area near Bristol, during the Rhaetian and the Tytherington site. (A) In the palaeogeographic map, about eight limestone islands (stippled) were scattered across a narrow seaway (blank). Fissure localities are marked by blue spots. Green squares show the locations of Penarth Group palynological profiles. Dotted line shows current Severn Estuary. (B) Geological map in the vicinity of Tytherington Quarry indicating fissure 2 and 4 positions. Ex17 is marked with an arrow. Note dash lines also outline quarries, fault lines run approximately N-S. Abbreviations: BRD, Black Rock Dolostone; BRL, Black Rock Limestone; Fm, Formation; Lst, Limestone; Sst, Sandstone. From Whiteside and Marshall (2008) and Klein et al. (2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

climatic and eustatic events (Walkden and Fraser, 1993). However, excepting sites 4, 5 and 5a of Fraser (1985), even at Cromhall exact sample locations are not recorded as specific points in the fissures. In general, although most Bristol fissure reptile fossils have been collected *in situ* (e.g. at Tytherington, Whiteside and Marshall, 2008) the treacherous rock faces, particularly in working quarries, have made up-sequence systematic sampling almost impossible.

On the basis of sedimentary associations, Fraser (1985), Walkden and Fraser (1993) and Simms et al. (1994) outlined a model of the formation and infilling of the Bristol sauropsid fissures that involved repeated episodes of deposition and erosion over an extended timespan, possibly from Carnian to early Rhaetian. This hypothesis was challenged by Whiteside (1983) and Whiteside and Marshall (2008) who argued that evidence from geomorphology, palynomorphs and animal fossils points instead to correlation with the start of the marine transgression of the early Rhaetian (and not earlier), and that this applies to the Tytherington fissures, as well as other Bristol fissures such as Cromhall, Durdham Down and Woodleaze (Whiteside et al., 2016).

Understanding the faunal successions of the Bristol fissures will help in understanding Late Triassic global faunas, especially in regard to the end-Triassic mass extinction (ETME), as emphasised by Whiteside and Marshall (2008). The duration, turnover patterns, and timing of the ETME are debated, as is the possibility of a spate of extinctions at the Norian-Rhaetian boundary (Tanner et al., 2004; Deenen et al., 2010; Schoene et al., 2010; Kent et al., 2017; Percival et al., 2017; Dunhill et al., 2018). There is evidence for a high rate of species turnover in both marine and terrestrial ecosystems during the Rhaetian (Benton, 1995; Tanner, 2018), with a phase of rapid turnover among marine organisms such as sharks (Cuny and Benton, 1999; Guinot et al., 2012), marine reptiles

(Thorne et al., 2011; Fischer et al., 2014) and multiple invertebrate phyla (Hallam, 2002). Conversely, only minor perturbations in taxonomic diversity and functional disparity affected bony fishes (Friedman and Sallan, 2012; Romano et al., 2014; Smithwick and Stubbs, 2018).

In the terrestrial realm tetrapod faunas underwent major restructuring. A significant decline in the diversity and disparity of crurotarsan archosaurs in the late Rhaetian coincided with an increase in dinosaur abundance and diversity, continuing a trend that had begun with the demise of the large dicynodonts in the Norian (Benton et al., 2014). Basal clades among lissamphibians, turtles, lepidosaurs, crocodylomorphs, and mammals also diversified at this time (Sues and Fraser, 2010; Benton et al., 2014), establishing the broad structure of modern terrestrial ecosystems.

Here we focus on the Tytherington site, where fissure 2 provides an extensive microvertebrate and invertebrate fossil record through the timeframe of fissure infilling (Whiteside, 1983; Whiteside and Marshall, 2008; van den Berg et al., 2012; Whiteside et al., 2016). By comparing this fossil biota with those of other parts of fissure 2 and the sauropsid fissures in general, we infer the impact of palaeoenvironmental factors on the fauna of a Late Triassic island ecosystem. We provide evidence on the palaeoenvironment and dating of the Tytherington Quarry fissures, as well as other similar Late Triassic sites in south-western England.

Institutional acronyms. BRSMG, Bristol Museum and Art Gallery, Bristol; BRSUG, University of Bristol, Geology Collection.

2. Geological setting

The extensive outcrops of Lower Carboniferous Limestone of the Severn Estuary area are penetrated by a number of Mesozoic

karstic fissure fills (Whiteside et al., 2016, Fig. 4), which are seen both in and north of Bristol (Tytherington, Cromhall, Durdham Down and Woodleaze; Fig. 1A).

The Lower Carboniferous Limestone of the Black Rock Limestone Subgroup was excavated in Tytherington Quarry (Ordnance Survey grid reference, ST 660890) for over 50 years. Quarrying activity resulted in the exposure of multiple vertical karstic fissures (Whiteside, 1983; Whiteside and Marshall, 2008; van den Berg et al., 2012). The focus of this paper is on fissure 2 (Fig. 1B), which has been destroyed by subsequent quarrying activity. In particular, the exposure at 17 m, which we term 'Ex17', is unique, as it was deeply-lying (about 20–30 m down) in the Carboniferous Limestone and represented part of a 26-m-long sequence along a fissure system (Whiteside and Marshall, 2008, fig. 9).

Fissure 2 is the only UK Late Triassic fissure site that is documented through multiple exposures as the Carboniferous Limestone was quarried in tier 3 of the quarry (Whiteside and Marshall, 2008). Therefore, the changes in morphology and

lithologies of the fissure (Fig. 2B, C) provide a unique context for the fossils not otherwise described in sauropsid fissures. The fissure is the type locality of *Diphydontosaurus avonis* Whiteside, 1986 and for a collection of bones of the 'Bristol dinosaur' *Thecodontosaurus antiquus*, found in the 1970s (Benton et al., 2012).

Fissure 2 occupied a NW-SE trending cavity formed by solutional action and joint widening within the Black Rock Limestone and near the boundary with the Black Rock Dolostone of the Black Rock Limestone Subgroup of the Lower Carboniferous. It is likely to have been continuous with fissure 4 (Fig. 1B) and lay sub-parallel to fissure 1 with which it was connected by small N-S joints and probably joined towards the SW.

Fissure 2 was filled with a variety of lithologies, including red and brown marls, silts, arenaceous limestones, conglomerates and breccias (Fig. 2). Clast sizes of the conglomerates and breccias range from a few millimetres to tens of centimetres. The larger-clast conglomerates and breccias are concentrated in the NW region of the fissure at the 0–8 m exposures, and smaller-clast
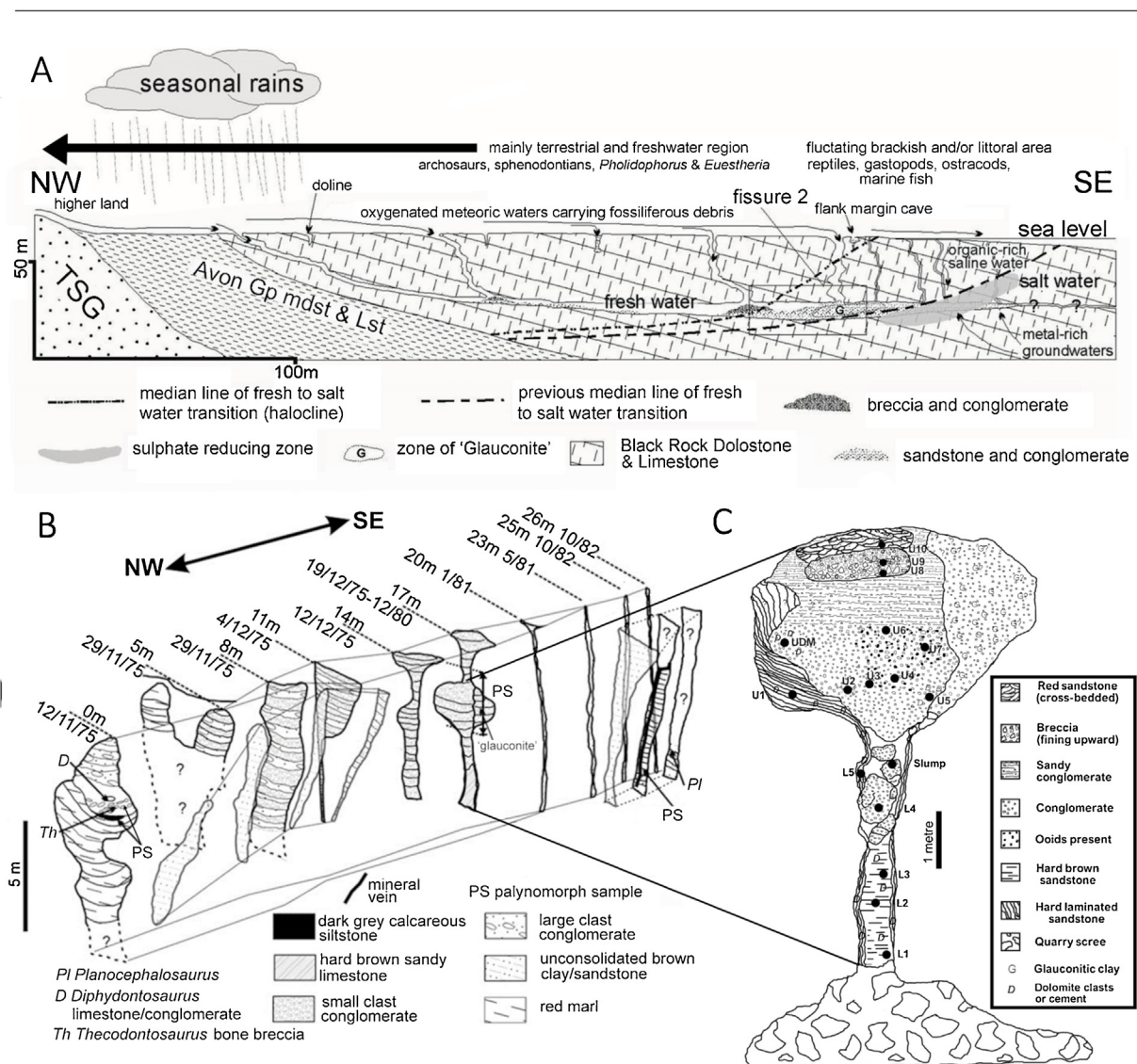

Fig. 2. Anatomy of fissure 2 at Tytherington Quarry, south Gloucestershire, U.K. (A) Reconstruction of the Fissure 2 palaeoprofile. Fissure fill deposits, cave formation, marine influences on sedimentation, fauna on the limestone surface and inferred meteoric freshwater flows are indicated. (B) Longitudinal cross-section of Fissure 2, showing sequentially quarried exposures along a NW to SE axis. The overall pattern is of a shift from large clast breccias and conglomerates at Ex0 towards smaller clast reddish conglomerates in the middle section, whereas siltstones and grey-black conglomerates predominate in the last sections (23–26 m). Ex17 is chiefly characterized by a circular structure that would have been located at the freshwater lens/saline water interface. From Whiteside (1983) and Whiteside and Marshall (2008). (C) Lithology of the 17 m exposure (Ex17) of Fissure 2. Rock types and positions of rock samples are indicated.

conglomerates predominate towards the SE (Fig. 2B). Many clasts include fossil bone (e.g. the *Thecodontosaurus* breccia) but there is also a range of metasomatically altered Carboniferous Limestones including dolomitised limestone, hard and soft limonitic dolomitised limestone and soft limonitic clay. The full range of metasomatism was observed *in situ* in fissure 7 (Fig. 3G), demonstrating that the varied clast lithologies largely derived from the Carboniferous Limestone. Some large rounded clasts match the

Triassic-aged 'Dolomitic Conglomerate' (Figs. 2B and 3 F), and the palynomorph dating of this fissure as Rhaetian (Whiteside and Marshall, 2008) indicates some episodes of high-energy terrestrial erosion.

The fill at Ex17 comprises mainly conglomerate, marl, breccia, and reworked sandy limestone (Whiteside, 1983; Whiteside and Marshall, 2008, table 1). Conglomerates with clasts, including reworked Carboniferous limestone, dominate in the upper section,
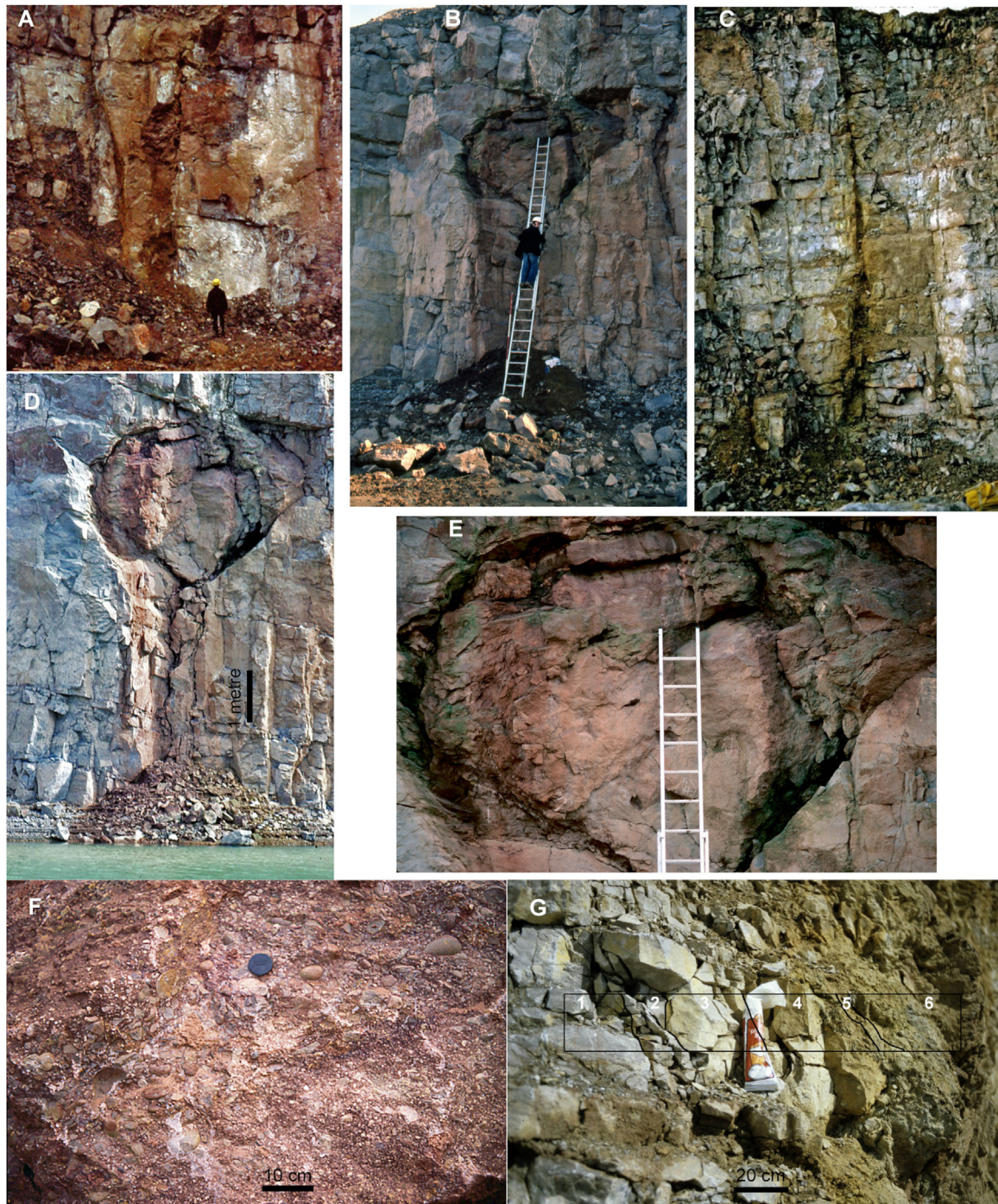
Fig. 3. Fissure 2 exposures in Tytherington Quarry, south Gloucestershire, U.K. (A) Fissure at 14 m, the exposure immediately before the site of the current study. (B) Fissure at Ex17 showing DIW collecting samples; two additional rocks originating from the glauconitic clay section were recovered from the scree at the base of the exposure. (C) Fissure exposure at 20 m, showing disappearance of the cavern in 1981. (D) Fissure full view before start of collection by .I.W, and C. Copp in 1980. (E) Close up of Ex17 cavern with chalked numbers of sample collection points visible. (F) Close up of large rounded clast (Dolomitic conglomerate) present at the 8 m exposure. (G) Fissure 7 showing in situ metasomatic change from the native Black Rock Limestone (1) forming the wall-rock, through hard white dolomitised Limestone (2), to limonite-stained and increasingly softer dolomitised limestone (3–5) and finally to yellow limonitic clay (6).

whereas the lowest samples consist primarily of marls, with the exception of the conglomeratic L4 and the 'slump' (Appendix: Table 1). The clastic rocks and paleosols of the fissure fill show signs of weathering by surface fresh waters and comprise fossil material from terrestrial taxa. However, the circular feature at the top of the fissure system (Fig. 3B, D, E) has been interpreted as the result of the influx of surface waters at the interface between a freshwater lens and an underlying saline layer (Whiteside and Robinson, 1983). As proposed by Whiteside (1983), the reworked terrestrial soils and rock clasts were probably carried by meteoric freshwater from the limestone surface of the palaeo-karst and deposited into the fissures where admixture with marine waters occurred. This mixing of meteoric and marine waters during fissure-fill sedimentation processes is consistent with what is observed on modern-day karstic limestone islands (e.g. Mylroie and Mylroie, 2007). The freshwater/ saline water mixing zone on modern islands (e.g. the Bahamas) is a region of high dissolution of limestone (Smart et al., 1988), and Mylroie and Mylroie (2013) describes cave formation at the top of freshwater lenses on Bahamian limestone islands, as well as near halocline and flank margins. The presence of layers of baroque dolomite crystals within a palynomorph-bearing Rhaetian rock from Fissure 2 provides further evidence of nearby saline waters (Whiteside and Marshall, 2008).

Dating of the infill of this fissure as lower Rhaetian (mid Westbury Formation) is based on four samples of palynomorphs found in the exposures at 0 m (termed Ex0 throughout; two samples), Ex17, and 25 m (Marshall and Whiteside, 1980; Whiteside, 1983; Whiteside and Marshall, 2008; Whiteside et al., 2016). The palynomorphs also revealed that there were mixed marine and terrestrial components in the fissure infill. A 'glauconitic clay' reported from this fissure (Whiteside and Robinson, 1983) provides further evidence that marine waters were present. Additional evidence for a marine influence on the Tytherington fissure fills includes Rhaetian fossil material from bony fishes (Whiteside, 1986; Whiteside and Marshall, 2008; van den Berg et al., 2012) as well as shark denticles and gastropod steinkerns (Whiteside and Marshall, 2008).

The Fissure 2 fossil fauna consists primarily of terrestrial Rhaetian taxa, but associated with reworked marine specimens from the Carboniferous Limestone (van den Berg et al., 2012). Triassic tetrapods include sphenodontians, possible crocodyliform bones, isolated archosaur teeth, and *Thecodontosaurus* remains, and the reworked Carboniferous specimens include conodonts, crinoids, and holocephalian elements (Whiteside and Marshall, 2008; van den Berg et al., 2012). In particular, prior to this study Ex17 had yielded bones and teeth of *Diphydontosaurus, Planocephalosaurus, Clevosaurus,* and *Thecodontosaurus*, steinkerns from Penarth Group gastropods, a *Gyrolepis* tooth, and a shark denticle from a possible hybodontoid (Whiteside and Marshall, 2008), in addition to palynomorphs and reworked Carboniferous material.

3. Materials and methods

3.1. Collection of rocks from fissure 2

The *Thecodontosaurus* and *Diphydontosaurus*-bearing rocks were dug out of the then newly exposed quarry face (0 m in Fig. 2B) in 1975 using a backhoe; the rocks were then transported to the University of Bristol. The Quarry Company, Amey Roadstone (now Hanson), conducted the digging and transport of the rocks free of charge and the operation was directed by Professor Bob Savage of the University of Bristol and Mel Bishop, the Quarry manager. Following further blasting and working of the quarry face, fossils from each subsequent exposure of Fissure 2 were collected. The fossils were frequently collected *in situ*, with access

to higher positions governed by the scree slope at the base. Other fossil-bearing rocks were collected from the scree slopes with identification of their origin made by eye or through binoculars.

From the start, the aim was to collect from all levels in the fissure system, but the dangers of rock fall generally prevented any attempt. Abseiling from the top was considered, but large cracks in the unstable quarry surface (of working level 2) above and around the fissure rendered any attempt too dangerous. The limestone face at Ex17 in fissure 2 was first quarried in 1975 but excavation was then halted at that level, and quarrying operations were concentrated elsewhere in the Tytherington Quarry complex. Pumping of water to lower the water table ceased and level 3 of the Quarry filled with water, reaching the mid upper cavern level, making access impossible. Pumping of the water re-commenced in 1980 to enable access to level 3 for further quarrying of the limestone. As fissure 2 had been weathered for five years, the face (Fig. 3D) had become more stable and it was decided that an attempt could be made at systematic sampling of the fissure up to about 6 m from the quarry floor. On October 11, 1980, DIW and Charles Copp (then of Bristol City Museum) took a ladder to the quarry and started systematically collecting rock samples (Figs. 2C, 3 B, E).

Rock samples (Appendices 1–2) were hammered out of the fissure and the position labelled with chalk numbers (Fig. 3E); the sample was either bagged by the collector while on the ladder or if the rock was at maximum arm's length it was dropped to the ground and collected by the other researcher. Two samples (UDM and U10) were collected at maximum stretch including the hammer, so chalk numbers could not be marked on the rock, but all other samples could be marked (Fig. 3E). Photographs were taken by telephoto lens to record the marked sample positions. Following the collection of samples U8–10, a substantial rock fall occurred, so systematic sampling ceased. Samples from the glauconite region (G1 and G2) were collected from the scree, and the position in the fissure located by viewing through binoculars. An attempt was also made to collect samples from the very top of the fissure which lay at the floor of the second quarried tier (Fig. 2B, 3 B), but large cracks prevented access.

3.2. Rock and fossil material

Geological samples from Tytherington Quarry have been under acid digestion and study since 1976, when D.I.W. undertook his PhD at the then Department of Geology of the University of Bristol (Whiteside, 1983). The rock samples collected *in situ* in 1980 constitute the basis for the present study.

The fossil elements obtained from the 17 samples are disarticulated, and most show little to moderate abrasion: the highly worn specimens from sample L4 are an exception. The colour of the bones varies from creamy white and yellow to brown, whereas teeth are mainly dark yellow or greenish in colour. Black gastropod steinkerns and other casts identified as from either crustaceans or bivalve molluscs were also recovered.

3.3. Rock processing and fossil sorting

The rock samples were prepared using the methods established by Whiteside (1983) and subsequently carried out by van den Berg et al. (2012). First, the surface of each sample was checked for exposed fossils to provide a first rough assessment of faunal contents. Treatment with Paraloid was deemed unnecessary as little bone was exposed.

The rocks were then immersed in a 5 % acetic acid solution. A tri-calcium orthophosphate buffer was added to prevent digestion of exposed bone surfaces. Following a 45–60 h treatment in the acid solution, samples were cleaned by rinsing in water. The

residue from each sample was then washed through sieves of mesh size 500 and 180 μm. The rocks were then immersed in buckets of water for a further 45–60 h. A drop of sodium hydroxide was added to each bucket to neutralize any remaining acid. Each sample underwent multiple cycles of acid, water cleaning, and neutralization.

After being collected by sieving, the residue was left to dry on filter papers positioned in funnels over small buckets. Once dried, the sediment was brushed into storage boxes. Source rock and filter size used were recorded for each container. Finally, the residue in each box was transferred to a standard microfossil grid. A Nikon C-LEDS binocular microscope was used to locate fossil specimens, which were placed in separate labelled storage boxes using a fine paintbrush. The residue collected through the filter of mesh size 180 μm yielded mainly fish teeth, bone shards, and invertebrate steinkerns, whereas lepidosaur jaws and the largest archosaur specimens were generally collected by the 500 μm mesh-size filter. Classifiable specimens were sorted into separate boxes according to broad morphotypes and identified on the basis of the literature.

For each taxon, representative specimens were photographed using a Leica M205C stereomicroscope equipped with a digital camera. A magnification factor of 1 was chosen for the main objective. Each specimen image was obtained by merging a stack of microphotographs using the Leica Application Suite – LAS v3.7 software. For each new stack, brightness, gamma and saturation were adjusted to optimise image quality. A black or white background was selected to enhance contrast. Measurements were made under the microscope using the embedded, adaptively adjusted scale bar. For isolated teeth, height was measured as the vertical line from the highest to the lowest preserved portion. Tooth width was measured at the broadest part of the crown.

3.4. Identifying fossil specimens and inferring species abundance

Of the over 4600 specimens obtained from acid digestion, 1523 were identified at some anatomical or taxonomic level; the rest consisted of isolated bone shards, or teeth that were fragmented beyond recognition. Wherever possible, lepidosaur and archosaur material was identified on the basis of characteristic shapes and sizes through comparisons with the literature. Osteichthyan teeth were identified by shape and/or the presence of an acrodin tip. Robust tooth plates with tubules were classified as holocephalian. Abundant crinoid stem ossicles were recovered but were generally unidentifiable due to weathering and crystallization. Mollusc and possible crustacean steinkerns were identified based on size and morphology. Sample G1 had been prepared and picked by DIW earlier, and the focus was on the coeval fossils, so reworked specimen counts in that sample are not dependable.

The assessment of species relative abundance was complicated by the fact that different taxa are represented by different fossils. For example, archosaurs and bony fishes are represented mainly by isolated teeth, with differences in morphotypes being attributable to either intraspecific, taxonomic or ontogenetic variation (e.g. Storrs, 1994; Heckert, 2004; Buckley and Currie, 2014). Difficulties arose even among closely related taxa. For instance, some samples yield a comparable number of *Clevosaurus* and *Diphydontosaurus* specimens, but the first is represented mainly by isolated teeth, the latter by numerous jawbones with multiple fused teeth. This likely reflects the resilience and hydrodynamic properties of different fossil specimens, with the smaller, lighter *Diphydontosaurus* specimens being washed over the limestone surface with relatively little damage, and the larger *Clevosaurus* bones fracturing into a number of robust fragments. One suggestion, made by Whiteside and Marshall (2008) and Whiteside et al. (2016), is that the animals were transported in part as articulated corpses either bloated or

mummified, which might have favoured the preservation of lighter individuals such as *Diphydontosaurus* in mid water, before disarticulation within the fissures. Alternatively, the *Diphydonto-saurus* may have lived near fissure entrances whereas *Clevosaurus* specimens were washed in from a wider area.

The results in the Faunal Composition section are based on a count of every taxonomically identifiable discrete specimen – including isolated teeth, bone fragments, and larger elements such as jawbones. This approach allows for a comparison of our results with those of van den Berg et al. (2012). However, it probably underestimates the relative abundance of those taxa represented by less fragmentary material.

4. Systematic palaeontology

4.1. Sphenodontians

The teeth and cranial material of sphenodontians could generally be identified to genus or species level based on published work (Fraser, 1982, 1986, 1988a; Whiteside, 1983, 1986; Fraser and Walkden, 1984; Whiteside and Marshall, 2008; Klein et al., 2015; Whiteside et al., 2016; Keeble et al., 2018). Identification of postcranial material proved more difficult, as it is often fragmentary and lacks visible synapomorphies. However, some postcranial elements were assigned to particular genera by comparisons with the relevant literature (Robinson, 1973; Whiteside, 1983; Fraser and Walkden, 1984; Fraser, 1988a, 1994; Klein et al., 2015; Keeble et al., 2018). Overall, about 550 sphenodontian fossils were recovered.
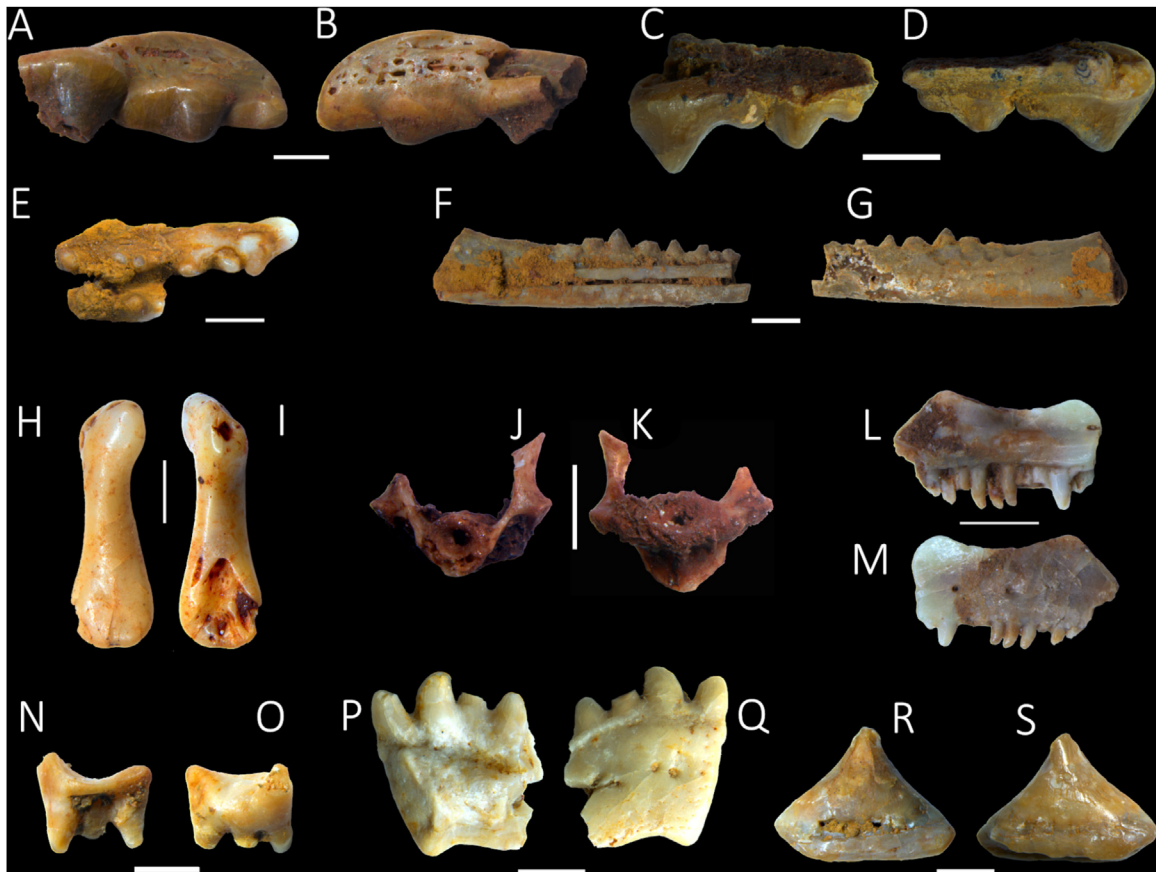
4.1.1. Clevosaurus sp.
Clevosaurus is represented by 230 specimens, including isolated teeth, jaw fragments, cranial bones and postcranial elements (Fig. 4A–E). The dentition is fully acrodont (Robinson, 1973, fig. 5C; Fraser, 1988a, fig.19). The dentary is deeper than in other Tytherington sphenodontians. Teeth are small, sharp and laterally compressed on the anterior dentary, whereas on the posterior half they are larger and robust, with a large posterior cusp and antero-lateral flanges (Fraser, 1988a, fig. 3). The maxillary teeth are laterally compressed, postero-laterally flanged, and chisel-like (Fig. 4A–D; Fraser, 1988a, fig. 22). Pterygoid teeth are stout and rounded and constitute well-defined parallel rows (Fig. 4E; Fraser, 1988a, fig. 16). Postcranial elements are robust, and larger than in *D. avonis*. *Clevosaurus* specimens are mostly preserved brown to light green.

4.1.2. Diphydontosaurus avonis *Whiteside, 1986*
Diphydontosaurus avonis is represented by 148 specimens, including jaw fragments, cranial bones and postcranial material (Fig. 4F–M). This taxon is characterized by pleurodont dentition on the premaxilla and the anterior parts of the dentary (Fig. 4F, G) and maxilla (Fig. 4L, M), and by acrodont teeth on the posterior portions of these elements (Whiteside, 1986, figs. 4, 6, 28). Tooth shape is variable: the pleurodont teeth are narrow and slightly recurved on the maxilla and mid-dentary, whereas acrodont teeth are conical and robust (Whiteside, 1986, fig. 4). Dentaries feature the diagnostic narrowed Meckelian fossa in the mid region (Fig. 4F; Whiteside, 1986, fig. 28). Postcranial elements are smaller and more gracile than those ascribable to other sphenodontians from Tytherington (Fig. 4H–K). Most of the *Diphydontosaurus* bones are white to light brown in colour.

4.1.3. Planocephalosaurus sp.
We identified 28 fragmentary specimens attributable to *Planocephalosaurus* (Fig. 4N–S). These show acrodont, radially ribbed dentition characteristic of the genus (Fraser, 1982, pl. 69,

Fig. 4. Representative sphenodontian material from the Ex17 of Fissure 2. (A, B) BRSUG 29956-6: Mid section of right maxilla of *Clevosaurus* sp. in labial (A) and lingual (B) views. (C, D) BRSUG 29956-7: Mid section of *Clevosaurus* sp. maxilla in lingual (C) and labial (B) views. (E) BRSUG 29956-8: *Clevosaurus* pterygoid in ventral view. (F, G) BRSUG 29956-1: *Diphydontosaurus avonis* dentary showing traces of ochreous matrix, in lingual (F) and labial (G) views. (H, I) BRSUG 29956-4: *Diphydontosaurus* humerus in anterior (H) and posterior (I) aspects. (J, K) BRSUG 29956-3: *Diphydontosaurus* vertebra in anterior (J) and postero-ventral (K) view. (L, M) BRSUG 29956-2: Right maxilla of *Diphydontosaurus avonis* in lingual (L) and labial (M) view. (N, O) BRSUG 29956-11: Right premaxilla of *Planocephalosaurus* sp. in lingual (N) and labial (O) views. (P, Q) BRSUG 29956-10: *Planocephalosaurus* dentary fragment in lingual (P) and labial (Q) views. (R, S) BRSUG 29956-9 *Planocephalosaurus* posterior dentary tooth in lingual (R) and labial (S) views. Scale bars equal 1 mm.

figs. 1–4, 6), although the ridges appear worn away in some specimens. Teeth are slightly recurved, pointed, and larger and more robust than in *Diphydontosaurus avonis*. These specimens probably represent *Planocephalosaurus robinsonae* (Fraser, 1982). However, one difference is that the Tytherington premaxilla (Fig. 4N, O) has three teeth, whereas type *Planocephalosaurus robinsonae* is characterised by four (Fraser, 1982, pl. 70, fig. 1). Most of the *Planocephalosaurus* material ranges in colour from light yellow to dark brown.
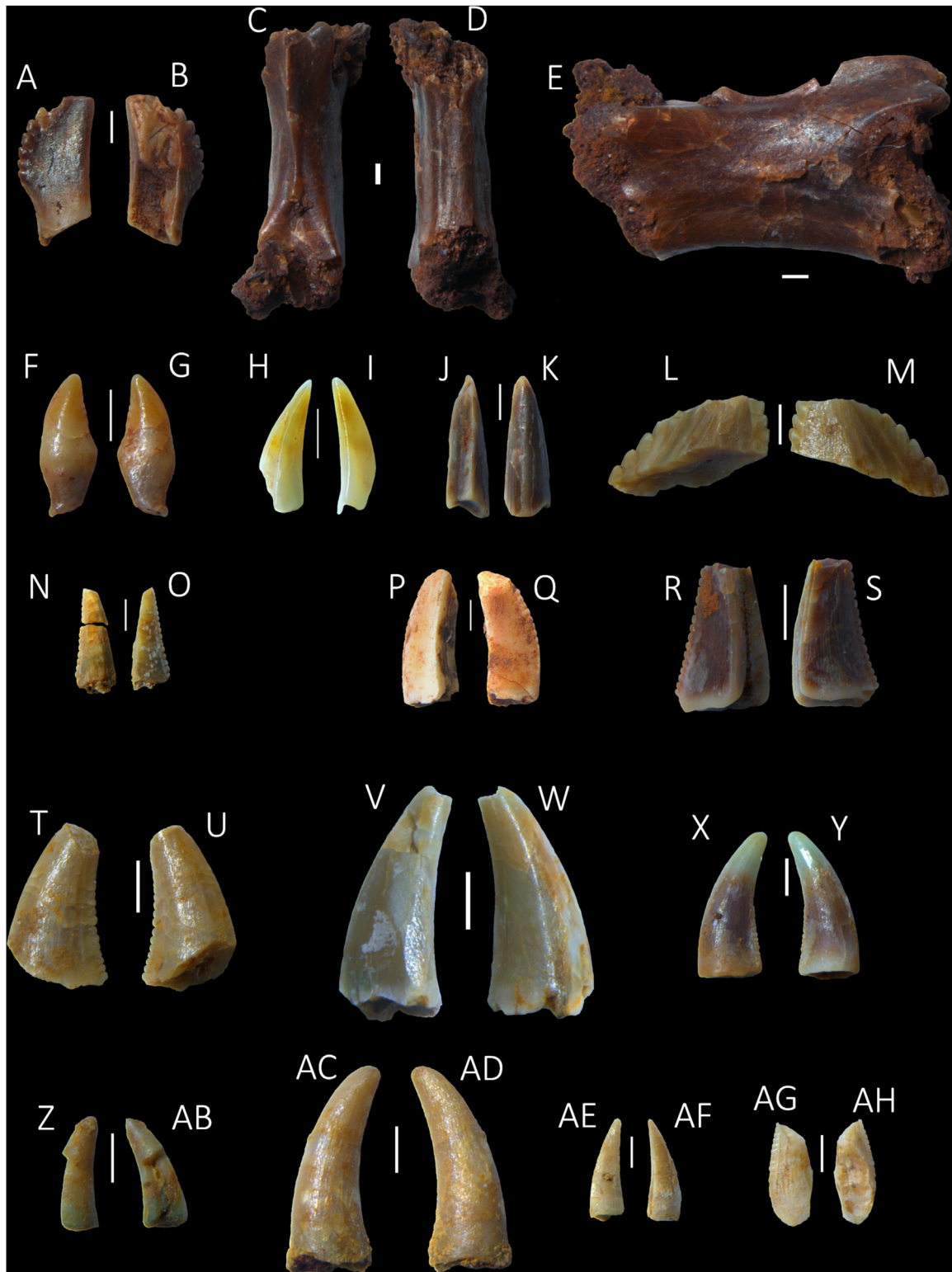
4.2. Archosaurs

Overall, 26 archosaur specimens were recovered. These include both teeth and bone fragments (Fig. 5). Some of the teeth are fragmented and unidentifiable; others could be assigned to distinct morphotypes on the basis of shape, size, and density of serrations. However, only *Thecodontosaurus* and *Terrestrisuchus* remains could be attributed to a named genus. Identification of isolated teeth lacking diagnostic features was not possible as archosaur teeth vary by ontogeny and position along the jaw (e.g. Heckert, 2004) and similar morphologies can be found in distantly related taxa (Nesbitt et al., 2013). Some of the serrated, recurved teeth of morphotypes C, G, I, J, and L could belong to small theropod dinosaurs similar to *Coelophysis* (Buckley and Currie, 2014, pp. 17–18) or *Liliensternus* (Godefroit and Knoll, 2003, fig. 6). A probable coelophysoid theropod was in fact reported by Whiteside and

Marshall (2008) from Tytherington. Other specimens, i.e. morphotypes F and H, may belong to prosauropods (Godefroit and Knoll, 2003, fig. 5), possibly *Pantydraco* (Keeble et al., 2018, fig. 12G and H). Large, triangular, serrated morphotypes such as G and I might represent pseudosuchians (Parker et al., 2005, fig. 2). Finally, morphotype E bears some similarities to the '*Paleosaurus*' teeth reported by Foffa et al. (2014, fig. 3M–P). In the absence of more complete material, these assignments remain tentative. Van den Berg et al. (2012) had already noted 15 morphotypes of archosaur teeth from Tytherington, and we equate our specimens with their classification where appropriate.

4.2.1. Archosaur morphotype A: Thecodontosaurus antiquus *Morris, 1843*

We found one tooth fragment referable with certainty to *Thecodontosaurus antiquus* (BRSUG 29956-12; Fig. 5A–B). The specimen is laterally compressed, and measures 2.3 mm in height and 1.1 mm in length. The fragment is split longitudinally, lacks a base and tip, and seems to represent the lateral margin of a leaf-shaped tooth. Serrations point from the root towards the tip (Benton et al., 2000, fig. 3G) and occur at a density of 4–5 per mm. In addition, a bone fragment referable to *Thecodontosaurus* was found. The size, shape, colour and texture of the specimen correspond to previously collected *Thecodontosaurus antiquus* material from Tytherington. However, it could not be identified further because of poor preservation (A. Ballell-Mayoral, pers. comm., 2019).

Fig. 5. Archosaur morphotypes from the Ex17 of Fissure 2. (A, B) BRSUG 29956-12: *Thecodontosaurus antiquus* tooth fragment with A, labial view and B, lingual view. (C, D, E) BRSUG 29956-13, *Terrestrisuchus* caudal vertebra in dorsal (C) ventral (D) and lateral (E) view. (F, G) BRSUG 29956-14, morphotype C in labial (F) and lingual (G) view. (H, I) BRSUG 29956-15, morphotype D with H, antero-lingual and I, postero-labial view. (J, K) BRSUG 29956-16, morphotype E with J, postero-lateral and K, anterior view. (L, M) BRSUG 29956-17, morphotype F with L, lingual and M, labial view. (N, O) BRSUG 29956-18, morphotype G with N, lingual and O, labial view. (P, Q) BRSUG 29956-19, morphotype H in two lateral views. (R, S) BRSUG 29956-20, morphotype I in labial (R) and lingual (S) view. (T, U) BRSUG 29956-21, morphotype J in labial (T) and lingual (U) view. (V, W) BRSUG 29956-22, morphotype K in lingual (V) and labial (W) view. (X, Y) BRSUG 29956-23, morphotype L in lingual (X) and labial (Y) view. (Z, AB) BRSUG 29956-24, morphotype M in two views. (AC, AD) BRSUG 29956-25, morphotype N in lingual (AC) and labial (AD) view. (AE, AF) BRSUG 29956-25, morphotype O in lingual (AE) and labial (AF) view. (AG, AH) BRSUG 29956-26, morphotype P in lateral (AG) and posterior (AH) view. Scale bars equal 0.5 mm.

4.2.2. Archosaur morphotype B: Terrestrisuchus sp.

Two vertebrae (BRSUG 29956-13 and BRSUG 29956-169) could be ascribed to *Terrestrisuchus* on the basis of size and morphology, and probably represent *T. gracilis* (Crush, 1984). Both specimens have elongated centra and lack lateral processes and can hence be identified as caudal vertebrae from the posterior 'Region 2' (Crush, 1984, fig. 13E–J). The neural spine of BRSUG 29956-13 (Fig. 5C–E) is low, extended, and rounded off posteriorly; this specimen thus appears to belong to the medial section of Region 2 (Crush, 1984, fig. 13F). BRSUG 29956-169 is more elongated and lacks an extended neural spine. It may belong to the distal section of Region 2 (Crush, 1984, fig. 13G–J), but is too abraded to be identified with certainty.

4.2.3. Archosaur morphotype C

BRSUG 29956-14 (Fig. 5F–G) is a small, slightly recurved tooth measuring 0.6 mm in height from base to tip, and 0.5 mm in length. This specimen is unique in completeness, and preserves most of its root section. The tooth is slightly laterally compressed, but relatively thicker along the midline of its width. Two small and rounded serrations are visible on the lower half of the posterior margin, with the hint of a third immediately above them. The surface appears smooth. The small size and incipient serration of this tooth suggest it might belong to a juvenile.

4.2.4. Archosaur morphotype D

BRSUG 29956-15 (Fig. 5H–I) is a longitudinally split, slightly recurved and slender tooth. The root is missing, and the preserved portion is 1.2 mm in height and 0.4 mm in length. The tooth appears almost triangular in cross-section. The surface is smooth and polished, probably as a result of abrasion, and serrations are lacking. However, minor indentations are visible along the posterior margin, possibly indicating the previous presence of serrations. This tooth resembles 'Morphotype 3' (van den Berg et al., 2012, fig. 3E–F), but it is smaller and slightly less slender.

4.2.5. Archosaur morphotype E

BRSUG 29956-16 (Fig. 5J–K) is a large, conical tooth split along it longitudinal axis. The base of the tooth is missing. The remainder measures 2 mm in height and 0.6 mm in length. Shallow ridges are visible at low density on the surface, but serrations are not present.

4.2.6. Archosaur morphotype F

BRSUG 29956-17 (Fig. 5L–M) consists of a cross-sectional fragment of a large, laterally compressed archosaur tooth. The fragment is 2 mm long and 1.4 mm tall. The surface is marked by shallow ridges at low density. Large serrations are present on both margins and occur at a density of 4 per mm anteriorly and 6 per mm posteriorly. The original tooth appears to have been triangular or leaf-shaped. This tooth almost certainly belongs to a sauropodomorph, most likely *Thecodontosaurus*.

4.2.7. Archosaur morphotype G

BRSUG 29956-18 (Fig. 5N–O) measures 1.7 mm in height and 0.6 mm in length.

The tooth is split and lacks the base and tip. Morphotype G teeth, which also comprise an additional three specimens, are slightly recurved, have extremely shallow grooves on the surface, and serrations on the posterior margin. These occur at a density of 8–14 per mm, suggesting a carnivorous animal. The density of serrations increases progressively towards the tip.

4.2.8. Archosaur morphotype H

BRSUG 29956-19 (Fig. 5P–Q) is a large, longitudinally split tooth fragment measuring 2.3 mm in height and 0.8 mm in length. The base and the tip are missing. The tooth is thick in cross-section, slightly recurved, and presents extremely shallow surface ridges. Smoothed, short serrations are present on the anterior margin at a density of 8 per mm. These reduce in height towards the base of the tooth.

4.2.9. Archosaur morphotype I

BRSUG 29956-20 (Fig. 5R–S) is a longitudinally split, large fragment missing its base and tip. The specimen measures 1.4 mm in height and 0.8 mm in length. It is robust, thick and slightly recurved, with irregular vertical surface markings. Serrations are present on the posterior margin at a density of 10–12 per mm. The serration density appears to decrease towards the tip of the tooth.

4.2.10. Archosaur morphotype J

BRSUG 29956-21 (Fig. 5T–U) is a fragment of a large, slightly recurved, and laterally compressed tooth. It is 1.4 mm tall and 1 mm long. Irregular, shallow vertical markings are visible on the surface. Serrations are present along the lower 80 % of the posterior margin at a density of approximately 11–14 per mm. Their density decreases towards the tip. Morphotype J is similar to morphotype G, but is slightly larger, more robust, and has a lower density of serrations. It might correspond to the fragmentary '*Palaeosaurus*' tooth reported by Whiteside and Marshall (2008, fig. 5h) from Fissure 2 (Ex0).

4.2.11. Archosaur morphotype K

BRSUG 29956-22 (Fig. 5V–W) is a recurved and slender tooth with an almost circular cross-section. It measures 2 mm in height and 0.5 mm in length. Its tip and base are missing. The surface is smooth, and the margins lack serrations.

4.2.12. Archosaur morphotype L

BRSUG 29956-23 (Fig. 5X–Y) is a slender, recurved, and laterally compressed tooth. It is 1.9 mm tall and 0.8 mm long. Shallow grooves mark the tooth from the tip to about 15 % of its height from the base. Serrations appear worn, and occur only on the lower half of the posterior margin at a density of 15 per mm. Their density decreases slightly towards the tip. This morphotype may correspond to 'Archosaur morphotype 7' of van den Berg et al. (2012, fig. 3M and N).

4.2.13. Archosaur morphotype M

BRSUG 29956-24 (Fig. 5Z–AB) is a small, recurved and very slender tooth. It lacks its base and is longitudinally fractured for the lower 70 % of its height. Its tip is heavily worn. The specimen measures 1.1 mm in height and 0.4 mm in length. The surface is smooth, and the margins lack serrations or other signs of dietary specializations. This morphotype resembles morphotype K, but it is smaller and less robust. It may correspond to 'Archosaur morphotype 15' of van den Berg et al. (2012, figs. 3AD and AE).

4.2.14. Archosaur morphotype N

BRSUG 29956-25 (Fig. 5AC–AD) is a slender, recurved, and slightly laterally compressed tooth. This specimen is well-preserved, with the base and tip semi-intact. It is large, measuring 2.3 mm in height and 0.9 mm in length. Shallow, irregular ridges run vertically on the surface. No serrations are visible, although the posterior margin is slightly irregular. Morphotype N resembles morphotype M; however, it is much larger and less smooth.

4.2.15. Archosaur morphotype O

BRSUG 29956-26 (Fig. 5AE–AF) is a slightly laterally compressed and recurved tooth. It is longitudinally split, and measures 1.7 mm in height and 0.5 mm in length. Irregular vertical markings are present on the surface but appear partly worn away. Very small,

worn serrations are distributed on the anterior margin at a density of 20 per mm.

4.2.16. Archosaur morphotype P

BRSUG 29956-27 (Fig. 5AG–AH) is a fragmentary and longitudinally split tooth. It is 1.5 mm tall and 0.6 mm long. This tooth is similar to Morphotype H. However, it is smaller, less robust, and has irregular vertical markings on the surface. Serrations are also denser: 14 per mm are visible on the anterior margin. As in morphotype H, they decrease in height towards the base.

4.3. Actinopterygii

Teeth of bony fishes are represented by 27 specimens. These range from semi-complete specimens retaining their fragile acrodin tips to small cross-sectional fragments. Some of the best-preserved material must have undergone little to no transport, whereas the fragmentary specimens may have been reworked or transported over greater distances. Whereas part of the material could not be identified taxonomically, the remainder was sorted into six morphotypes (Fig. 6).
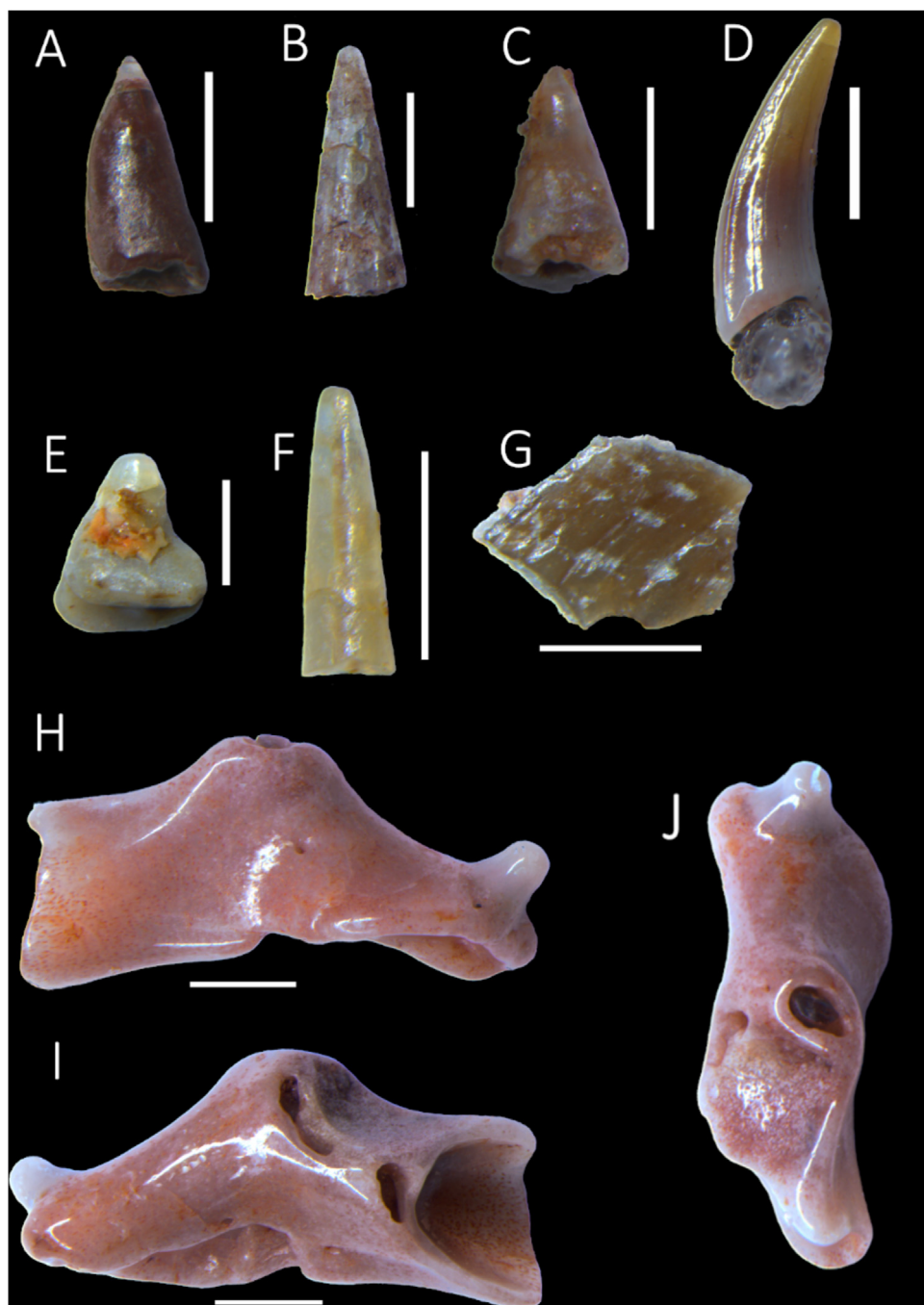
Fig. 6. Representative bony fish specimens. (A) BRSUG 29956-28, *Gyrolepis albertii* tooth with partially, darkened surface. (B) BRSUG 29956-29, morphotype 2. (C) BRSUG 29956-30, morphotype 3. (D) BRSUG 29956-31, morphotype 4. (E) BRSUG 29956-32, morphotype 5 (?*Lepidotes* sp.). (F) BRSUG 29956-33, morphotype 6. (G) BRSUG 29956-223, osteichthyan scales. (H, I, J) BRSUG 29956-185, unidentified bony fish element in three views. Scale bars represent 0.5 mm.

4.3.1. Gyrolepis albertii Agassiz, 1835

Of the identifiable actinopterygian teeth, 19 are ascribed to *Gyrolepis albertii*. These are mostly slightly sigmoidal or conical and decrease in width towards the tip (Fig. 6A). Thickness, degree of curvature and length vary. The tooth surface appears smooth. Where present, the translucent enamel cap is straight, conical, and unornamented (Cross et al., 2018, fig. 10A). The length of the cap varies from 15 % to 35 % of total tooth length. Most of the *Gyrolepis* specimens may be the same as the Fissure 2 'Fish morphotype 1' described by van den Berg et al. (2012, fig. 4A).

4.3.2. Actinopterygian morphotype 2

Actinopterygian morphotype 2 is represented by BRSUG 29956-29 (Fig. 6B), a conical tooth fragment 1.2 mm tall and 0.5 mm long. This specimen lacks the base and is heavily marked by vertical ridges. Although weathered, it appears translucent, and may be the acrodin cap of a *Birgeria*-type *Severnichthys* tooth (Storrs, 1994, pp. 229–234).

4.3.3. Actinopterygian morphotype 3

Morphotype 3 is represented by BRSUG 29956-30 (Fig. 6C), a partial tooth 0.8 mm tall and 0.5 mm long. The base is missing, and the entire surface is heavily worn. Nonetheless, vertical grooves are visible on the conical acrodin cap, which represents about half of the total length of the specimen. A weakly defined neck separates the acrodin cap from the lower portion. This morphotype might represent a *Saurichthys*-type *Severnichthys* tooth (Storrs, 1994, pp. 229–234) but could not be identified with certainty.

4.3.4. Actinopterygian morphotype 4

BRSUG 29956-31, the only specimen ascribable to Morphotype 4 (Fig. 6D), is the only actinopterygian specimen found in the lower section rock samples. This tooth is semi-complete, and measures 1.1 mm in height and in 0.4 mm length. It is slender and curved but differs from comparable *Gyrolepis* teeth (e.g. Nordén et al., 2015, fig. 9A) in lacking a discernible neck between the enamel cap and the lower section. The surface is highly polished, but shallow, parallel vertical grooves are visible. This tooth might belong to *Pholidophorus*, which has previously been reported from Tytherington Fissure 2 (Whiteside and Marshall, 2008, p. 110).

4.3.5. Actinopterygian morphotype 5: Lepidotes sp.

BRSUG 29956-32 (Fig. 6E) is a globular, unornamented tooth 0.8 mm tall and 0.7 mm long. The specimen has a relatively large, square acrodin cap, and a wide semi-rectangular base. Size and morphology resemble those of *Lepidotes* specimens from the British Rhaetian (e.g. Nordén et al., 2015, fig. 9I; Mears et al., 2016, fig. 7I–J), although the characteristic finely striated root is lacking.

4.3.6. Actinopterygian morphotype 6

BRSUG 29956-33 (Fig. 6F) is a 0.7 mm tall and 0.2 mm long actinopterygian tooth section, missing its base. The specimen is conical, slender, and translucent, and might represent an isolated acrodin cap. Its surface is highly polished.

4.3.7. Osteichthyan scales

BRSUG 29956-223 (Fig. 6G) is a fragment of fossil bony fish integument. It comprises more than ten heavily polished, rhomboidal ganoid scales. These may belong to *Pholidophorus*, which was previously recorded at Tytherington by Whiteside and Marshall (2008). Parallel striations are visible on some of the scales. The bony layer underlying the superficial ganoin cover is preserved. The specimen is light in colour.

4.3.8. Osteichthyan skull element

BRSUG 29956-185 (Fig. 6H–J) is an unidentified skeletal element. Its morphology and texture suggest it may be an osteichthyan skull bone, possibly a supratemporal. However, it seems to be heavily abraded and polished, and it could not be identified.

4.4. Elasmobranchs

Sparse elasmobranch remains consisting of isolated teeth and denticles were recovered from the upper section samples. These range in colour from dark brown to light purple. Most specimens are highly worn, and probably represent reworked Carboniferous taxa from the limestone underlying the fissure. A variety of morphotypes (Fig. 7) could be defined, but a taxonomic identification is seldom possible. In summary, possibly only two of the illustrated specimens (Fig. 7C, G) are from the Late Triassic, whereas the other eight (Fig. 7A, B, D–F, H–J) are likely reworked from the Carboniferous.

4.4.1. Ctenacanthid denticles

Three specimens were identified as dermal denticles from Ctenacanthidae, on the basis of similarities with described taxa (Mutt and Rieber, 2005, fig. 6; Landon et al., 2017, fig. 5P and Q). BRSUG 29956-45 (Morphotype 1; Fig. 7A) has a robust, multi-cusped crown sitting on a circular basal plate. The cusps are wide, slightly recurved and laterally fused. BRSUG 29956-44 is a different morphotype (Morphotype 2; Fig. 7B) comprising two specimens from U4 and U1. Whereas the U1 denticle is fragmentary, BRSUG 29956-44 is relatively well preserved and has a narrow and semi-conical lower section. Part of the pedicle appears to be missing. The cusps are partially fused, elongated and recurved, giving the denticle a lanceolate appearance.

In terms of identity, these could be ctenacanthid denticles either from the Carboniferous or Triassic, as the group was long-lived. The somewhat expanded basal plates are reminiscent of Carboniferous examples, and the specimen in Fig. 7B is certainly a Carboniferous symmoriiform branchial denticle, often called *Stemmatias* in the older literature (cf. Ginter et al., 2015, fig. 15D).

4.4.2. Hybodontoid fin spines

Two partial selachian dorsal fin spines were recovered, represented by BRSUG 29956-46 (Fig. 7C). Both are incomplete and lack a tip and base. The surface is marked by deep vertical ridges lacking tuberculated ornaments, suggesting that these specimens probably belonged to hybodontiforms (Maisey, 1986, fig. 9; Lakin et al., 2016, fig. 8 C) and not ctenacanthids (Maisey, 1981, pp. 1–17). However, the downturned posterior denticles diagnostic of hybodontiforms are not visible, possibly as a consequence of abrasion.

4.4.3. Tooth morphotype A

A single specimen (BRSUG 29956-47; Fig. 7D) could be referred to this morphotype. This tooth has a semi-rectangular and partially missing peduncle. The central cusp is recurved, pointed, and flanked by two pairs of tines measuring less than half its height. The labial wall of the central cusp is perforated by foramina, whereas the lingual side is heavily worn. The two basolabial projections in the root indicate that this tooth belongs to a reworked cladodont from the Carboniferous (Ginter et al., 2015, fig. 7).

4.4.4. Tooth morphotype B: Thrinacodus sp.

Thrinacodus is a Palaeozoic genus represented by multiple isolated teeth found across the upper section samples, which show a morphological correspondence with previously recorded
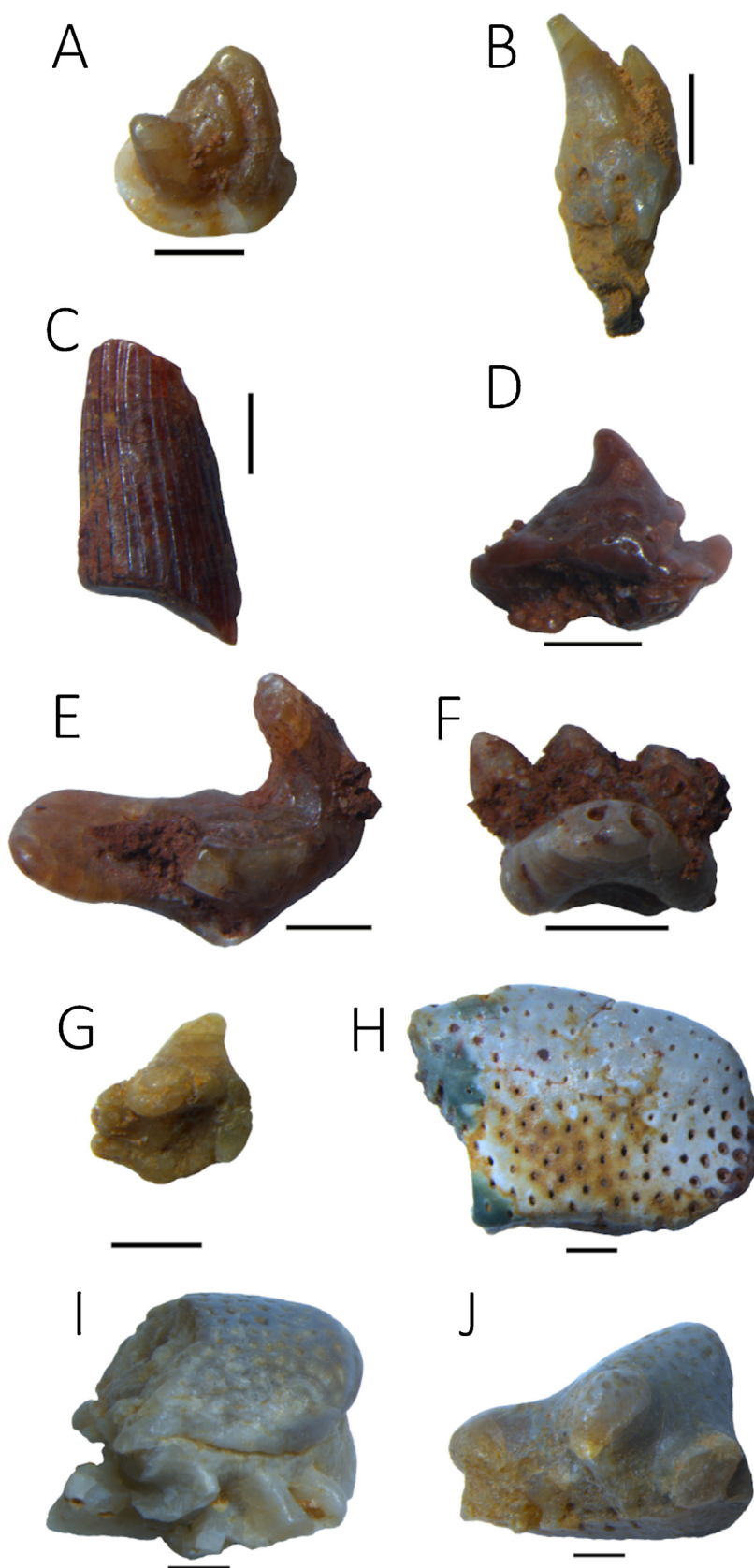
Fig. 7. Representative elasmobranch specimens. (A) BRSUG 29956-45, ctenacanthid dermal denticle (Morphotype 1, probably reworked from the Carboniferous). (B) BRSUG 29956- 44, ctenacanthid dermal denticle (Morphotype 2, *Stemmatias* type, reworked from Carboniferous). (C) BRSUG 29956-46, hybodontoid fin spine. (D) BRSUG 29956-47, tooth morphotype A – a possible cladodontomorph. (E) BRSUG 29956- 43, *Thrinacodus* tooth. (F) BRSUG 29956-49, possible Triassic *Hybodus* (=*Rhomphaiodon*) *minor* tooth, or Carboniferous euselcchian tooth. (G) BRSUG 29956-48, 'dermal denticle B'. (H–J) Chimaeroid elements (BRSUG 29956-52 BRSUG 29956-50, BRSUG 29956-51). Scale bars represent 0.5 mm.

specimens from the UK (Duffin, 1993) North America, and Australia (Ginter and Turner, 2010, fig. 3F–H). The most complete of the Fissure 2 specimens, BRSUG 29956-43 (Fig. 7E), is a 2.1 mm long specimen referable to *T. ferox* (Turner, 1982), a taxon that had previously been reported from Fissure 2 (van den Berg et al., 2012, fig. 5A). This specimen has an asymmetrical crown, with two slender and recurved cusps preserved, one of which is laterally oriented, the other semi-vertical. The surface of the latter cusp bears shallow longitudinal ridges. The tooth base is elongate and extended labiolingually, and a large foramen is present on the underside.

4.4.5. Tooth morphotype C: Hybodus *sp.*

BRSUG 29956-49 (Fig. 7F) is a tricuspid elasmobranch tooth with a wide, semi-circular root. The cusps are pointed, robust, and partially fused at the base, and decrease in height anteriorly. Parallel vertical ridges run on the lingual surface of the cusps, and the labial side of the root is perforated by large, sparse foramina. Comparisons (e.g. BRSMG Cf 2934) indicate that this tooth may have belonged to *Hybodus*, possibly *H. (=Rhomphaiodon) minor* (Agassiz, 1833), a Triassic form. Alternatively, the concave undersurface of the tooth suggest it might be a reworked Carboniferous euselachian tooth (cf. Ginter et al., 2015, fig. 14A) with a lingually extended root.

4.4.6. 'Dermal Denticle B'

BRSUG 29956-48 (Fig. 7G) is a recurved, heavily worn denticle with a globular base. It measures about 0.8 mm in height and 0.9 mm in length. This specimen is reminiscent of 'Dermal Denticle B' from the Filton West Chord (Landon et al., 2017, fig. 5K and L), but is too poorly preserved to allow for a conclusive identification.

4.4.7. Holocephalian elements

About 160 fragments of holocephalian tooth plates (Fig. 7H–J) were recovered. These vary greatly in size, shape, and colour, ranging from light grey to brown to light purple. The tooth plates bear tubules, which vary in size and density, crossing their width. It is likely that there are multiple taxa, but the material is too fragmentary to enable identification. It is possible that they are Triassic myriacanthid holocephalians. However, these are usually rare and quite delicate, so the robustness of our specimens suggests they represent reworked Carboniferous specimens like those assigned by Whiteside (1983) to the bradyodont taxa *Psephodus* and *Helodus*.

4.5. Gastropods

We recovered 147 internal casts (steinkerns) of gastropods. Although some of these are highly fragmented, most are minimally damaged, often missing only the apex. Most of these can be identified with taxa from the Penarth Group described by Swift and Martill (1999). All steinkerns are uniformly black in colour, suggesting that fossilization may have occurred under mainly anoxic conditions (Whiteside and Marshall, 2008, p. 132). Two taxa were identified: *Chemnitzia granum* and *Crossostoma* sp. (Fig. 8), the latter not previously documented from the Rhaetian.

4.5.1. Chemnitzia granum

Chemnitzia granum is represented by 14 fragmentary, turreted steinkerns about 1 mm long (Fig. 8A–B). The whorls are smooth and moderately convex. The suture is impressed and shouldered, and no axial ornaments or growth lines are visible. The genus *Chemnitzia* is recorded from the Triassic to the present day, with rich records in the Cenozoic, and so it is unclear whether the Triassic examples really pertain to the modern genus, or whether the name is given rather widely to any high-spired gastropod, but
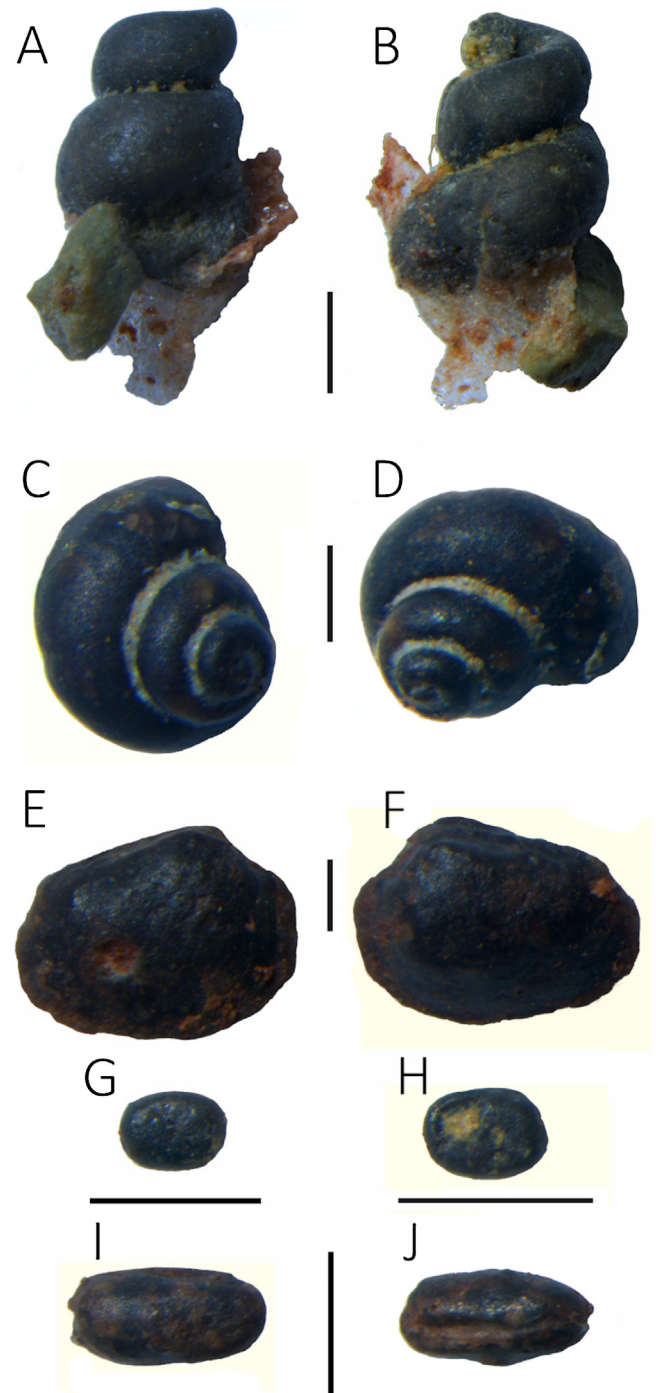
Fig. 8. Representative steinkern specimens, including all the different morphotypes recovered from the Ex17 samples. (A, B) BRSUG 29956-38, *Cheminitzia granum*. Notice the marine glauconitic clay matrix. (C, D) BRSUG 29956-39, *Crossostoma* sp. (E, F) BRSUG 29956-37, unidentified two-valved steinkern. (G, H) BRSUG 29956-36, Ostracoda indet. (I, J) BRSUG 29956-35, *Darwinula* sp. Scale bars represent 0.2 mm, except for (A, B) and (I, J) where they equal 0.5 mm.

we follow normal practice in identifying this taxon by comparison with other Triassic and Jurassic records.

4.5.2. Crossostoma *sp.*

Crossostoma is the most abundant molluscan taxon of the exposure, numbering over 130 specimens. Steinkerns are generally less than 1 mm long. The overall shape is globular, obtuse and depressed with convex whorls. The whorls are smooth, with

thefirst comprising from about half to two-thirds of the shell's total length. The shell aperture is broad and semi-circular. The *Crossostoma* specimens recovered from the exposure, such as BRSUG 29956-39 (Fig. 8C–D) can be tentatively assigned to *Crossostoma reflexilabrum* (d'Orbigny, 1850). Since only the largest *C. reflexilabrum* individuals show the diagnostic upturned marginal lip, the small size of the Tytherington specimens may well explain the absence of this trait. *C. reflexilabrum* has also been found in a fissure in a disused quarry near Stubb's Wood, Merehead (ST 698437), which has been dated as Pliensbachian in age (Copp, unpublished manuscript) and from a 'Liassic vein' at Holwell Quarry (Moore, 1867). The presence of *Crossostoma* specimens in a Late Triassic fissure deposit extends the known temporal range of this taxon and indicates its persistence across the ETME.

4.6. Unidentified 'bivalve' steinkerns

A total of 18 specimens reminiscent of blackened bivalve steinkerns (Fig. 8E–F) were recovered. These carapace casts are less than 1 mm long. The shape is slightly variable, but generally sub-ovate. The umbo is well-defined and positioned anteriorly. The steinkern surface is black and polished, with no visible ridges or ornamentations. An identification was not possible because there are no surface markings, muscle scars, or other diagnostic features. These steinkerns could represent either small *Pteromya*-type bivalves figured by Swift and Martill (1999) or the conchostracan crustacean *Euestheria,* which has been reported previously from Tytherington (Whiteside and Marshall, 2008; Whiteside et al., 2016) and the nearby Cromhall Quarry (Morton et al., 2017).

4.7. Crustaceans

Crustaceans were found in smaller numbers than gastropods. The steinkerns are uniformly black, small, compact, and generally intact. The two morphotypes are ascribed to ostracods (Fig. 8G–J).

4.7.1. Ostracoda indet

Two specimens recovered from the U5 sample are small (∼0.3 mm long) ostracods. These steinkerns (Fig. 8G–H) are almost circular in outline and slightly laterally flattened. Their surface is black and unornamented.

4.7.2. Darwinula sp.

Darwinula specimens were found exclusively in the detrital marl sample of the upper section (UDM). These ostracod steinkerns are around 0.8 mm long, elongated, and lack any ornament or marginal features (Fig. 8I–J). The posterior section appears higher and more laterally inflated than the anterior.

4.8. Other fossils

A possible blackened ichthyosaur tooth (BRSUG 29956-34; Fig. 9A) was recovered from sample U5. This specimen is abraded and fragmentary, lacking a root and tip, and might instead represent a *Birgeria*-type *Severnichthys* tooth. However, its smooth base, opaque surface, and the marked, closely-spaced ridges suggest ichthyosaurian affinities (cf. Allard et al., 2015, fig. 8A–C).

In addition, a conodont specimen (BRSUG 29956-42; Fig. 9B) was recovered from the L4 sample. This element is blade-like in shape. Its lower rim and basal cavity are slightly recurved, and the upper margin is smooth and crescent-shaped. The surface is heavily worn, suggesting a Carboniferous origin. This element may correspond to 'Conodont Morphotype 3' (van den Berg et al., 2012, fig. 5F).

Abundant crinoid ossicles were also found in most fissure fill samples. Most of these were highly weathered and crystallized, with colours ranging from white to dark brown. A range of different morphs was recovered, including circular, spike-bearing and stellate elements (Fig. 9C–E). These elements are common in the surrounding Carboniferous limestone, and the circular ones (Fig. 9E) may represent reworked taxa (van den Berg et al., 2012, p. 645), but the stellate examples (Fig. 9C, D) are reminiscent of
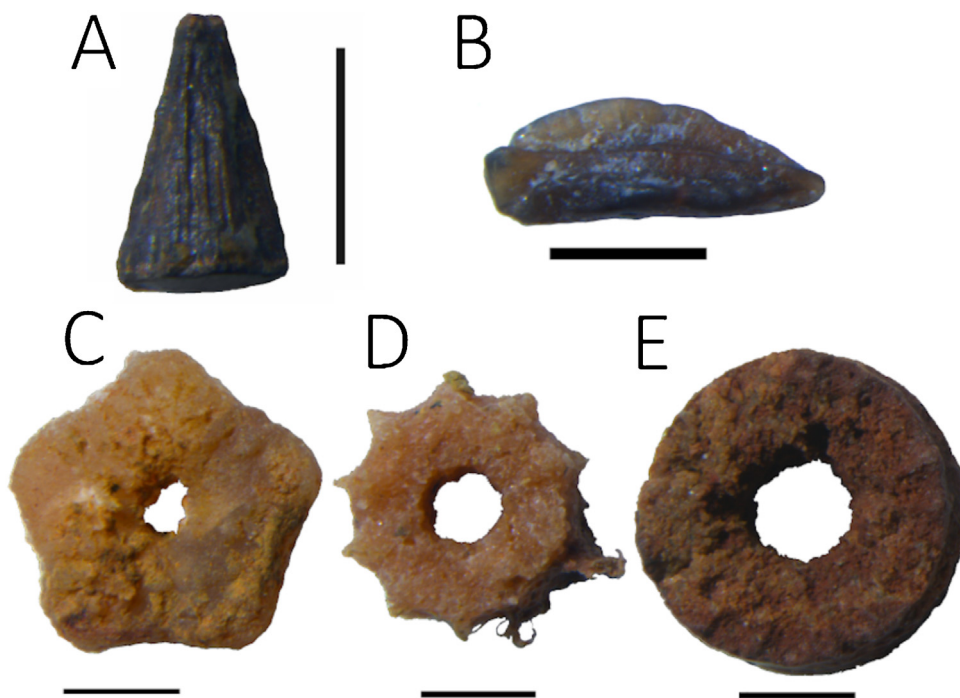
Fig. 9. Other fossil morphotypes from the Ex17 samples. (A) BRSUG 29956-34, 'Ichthyosaur' (possibly *Birgeria*) tooth. (B) BRSUG 29956-42, conodont element. (C) BRSUG 29956-41, asteriform crinoid ossicle. (D) BRSUG 29956-40, crinoid ossicle with radial spikes. (E) BRSUG 29956-143, circular crinoid ossicle. Scale bars equal 0.5 mm.

isocrinoids, an exclusively Mesozoic group, and so these may be from the Late Triassic (Landon et al., 2017, fig. 7J, K).

5. Faunal composition and implications for fissure formation and filling

5.1. General faunal composition and inferred palaeoenvironment

Considering the pattern of terrestrial versus coeval marine components (including *Gyrolepis* and the gastropods), the latter are far rarer in the lower fissure samples (*c.* 10%) and absent in U1, with only L4 yielding any significant numbers. Excepting U10, where only one Triassic fossil (in total) was recorded, the marine contribution to the cavern fossils (upper section) is significant, varying from 13.4 % (U4) to the very high 77.8 % of U9 (Appendix 4).

Sphenodontians comprise the principal terrestrial component in Ex17 and are found from the bottom sample (L1) to the top (U10). However, sphenodontian fossils are only found in two of the six lower fissure samples and almost all of these are in the conglomerate of L4. The bones in L4 are distinctive in being fragmentary and highly polished compared with all other samples. This suggests that they were transported further or in a higher energy flow, such as in a tropical rainstorm. In addition, polishing could have occurred during transit in narrow rocky passages, compared to falling through a more vertical water column.

Comparing the component of terrestrial tetrapods with remanié fossils for each section highlights a much lower percentage of reworked elements in the lower fissure region (19 %) compared to the upper (cavern) part of 58.2 %. There appears to be little pattern in terms of proportions of reworked fossils throughout the upper parts of the fissure. The neighbouring samples U4, U5 and U7 do have the three highest reworked components, but the proportion of remanié fossils in the cavern varies from 42.4 to 73.5% except in the glauconitic clay region, which has a low of about 21 %. However, this low value could reflect the fact that the sample was processed differently than the others, and D.I.W. focussed on extracting coeval fossils.

As the reworked components derive entirely from the Black Rock Limestones, higher percentages and numbers of reworked fossils suggest periods of greater erosion with the fossils dissolving out of the limestone by meteoric surface waters or through mixing freshwater with saline waters. Although some of the dissolution might have occurred within cavities, the relatively well preserved accompanying terrestrial tetrapod bones and teeth suggest that most of the remanié elements originated in surface rocks. This may indicate an enhanced energy input carrying more debris at the time of filling of the upper part of the fissure, possibly from higher rainfall (or at least a greater flow of freshwater) and collapse of fissure cavities due to decreasing salinity and higher partial pressures of CO_2. The highest proportions of reworked fossils occur in U4, U5 and U7 in the mid lower cavern, which probably indicates a time of great surface erosion and presumably rapid infilling.

5.2. Implications for fissure formation: dissolution of the limestone in the cavern region

It is clear that filling of the fissure Ex17 occurred in a mixing zone of a freshwater lens and marine waters, as described by Whiteside and Robinson (1983). Recognising that the upper fissure fill has a greater marine influence and a higher proportion of reworked fossils, it is possible to infer the development of the fissure. We know from the preceding exposure at 14 m (Fig. 3A) and the following exposure at 20 m (Fig. 3C) that the cavern was a localised development. The maximum Ex17 cavern size was about 3.25 m across. The cave was sub-spherical, but treating it as a sphere gives an estimated cavity volume of about 18 m³.

We considered how long it would take to form a limestone cavern of this size at the edge of a freshwater lens bordering seawater. The calculation is based on experiments in determining dissolution and precipitation rates with different proportions of artificial sea water or saltwater and freshwater containing calcium carbonate. According to Singurindy et al. (2004, table 2), for high proportions of freshwater (70 % and 80 % respectively), dissolution rates of calcium carbonate were $6.2–7.2 \times 10^{-4}$ kg/m³/day. If these proportions pertained in the fissure during cavity formation, which is reasonable considering that the lower fissure has little marine component, then the cavity could have been fully formed in fewer than a few hundred years assuming a stable palaeoenvironment. If the mixing zone had only 30 % freshwater, the dissolution under stable conditions could have been achieved in fewer than 1000 years. However, the freshwater lens probably fluctuated in size as recharge by surface runoff was seasonal (the presence of *Euesrheria,* living in surface pools or fissure entrances, in different fissures at Tytherington is indicative of wet and dry seasons, Whiteside and Marshall, 2008) and entry and outflow from the cavern might have been blocked at times by wall and roof collapses. Even with these considerations, it is reasonable to conclude that cavern formation likely took a few thousand years. Some substantially larger (10 times the volume of Ex17) Bahamian flank margin caves are known to have formed in 9000 years (Mylroie and Mylroie, 2013; Mylroie, pers. comm.).

The rate of cave formation by dissolution could be affected by pH. Whiteside and Marshall (2008) suggested that dissolution could have been accelerated by a low pH resulting from acidified water. The water might have been acidified by oxidation of rising gaseous hydrogen sulphide released by sulphate-reducing bacteria lying near the halocline in the mixing zone, as recorded in the Andros Island blue holes by Smart et al. (1988). Organic debris from the Tytherington limestone surface would have provided the energy source for these bacteria. Whitaker and Smart (2007) also demonstrate that high partial pressures (P_{CO2}), which would result in high dissolution rates, are found in the freshwater lens derived from meteoric water on Andros Island, Bahamas; they suggest that this is produced by oxidation of organic carbon originating from the surface biosphere and soils. Field observations show that dissolution rates of limestone in the freshwater/seawater mixing zone can be very high. For example, the Yucatán carbonate platform could disappear in 5000 years (Singurindy et al., 2004). We conclude that cavern formation of the exposure shown in Fig. 3 was likely remarkably quick (thousands to a few thousand years) and provided a large receptacle for the dumping of debris.

5.3. Implications for fissure formation: sequence of fissure filling in Ex17

The fissure is formed along a joint (Fig. 3A–D). The lower part of the fissure has vertical or sub-vertically oriented layered sediment that clings to the limestone wall-rock, including to solutional horizontal grooves on the Carboniferous Limestone. We postulate that this lithology of clays and silts was the first to deposit and partially consolidate in the fissure. The sediments would have been carried in a suspension load that penetrated the narrow passages in the limestone. As a result of the narrow passages no fossiliferous material was carried to this deep part of the limestone, but it would have been dumped higher in the passages or abraded so that no recognisable elements remained. Sample L5 (Appendix 2) represents this lithology; it is well layered, fine grained and hard, probably from dolomite cement. Dolomite is known to have precipitated directly in fissure 2 in the Rhaetian (Whiteside and Marshall, 2008, fig. 8g) and metasomatic changes in fissure 7 (Fig. 3G) demonstrate that the Carboniferous Limestone was dolomitised either by geochemical action in the freshwater/ seawater mixing zone or by hydrothermal activity.

The cavern developed in the freshwater/seawater mixing zone above the lower section of the fissure, perhaps by paragenesis (where dissolution of limestone occurs above the sediment-covered floor; Farrant and Smart, 2011). Sediment, now containing conglomerates as well as clays and silts, continued to thicken on the cavern floor. A tectonic opening of the joint was followed by a concomitant collapse of the sediments into the lower part of the fissure (samples L1-L4 and the slump). The partially consolidated sediment of L5 already in the lower fissure is preserved as the semi-vertical layer bordering the wall-rock. Most of the sediments in this part of the fissure were dolomitised.

Cavern formation probably continued by paragenesis, but sedimentation would have increased as there was greater access into the cavern because entry fissures had widened. The earliest of the sediments is represented by U1 from the bottom left-hand side of the cavern. The widening of the entry fissure resulted either from tectonic activity or by further dissolution of carbonates by meteoric waters leading to wall and roof collapse. Some of the rockfall might have contributed to the sedimentary infill of the cavern; however, the high proportion of terrestrial reptile fossils and coeval marine fauna (at or above 50 % excepting U4 and U7; Appendix 4) indicates that debris from the limestone surface, including the reworked fossils, constitute much of the fissure fill. The cavern filling consists predominantly of conglomerates, including bone conglomerates, although there are breccias, silts, marls and clays including illite as well as the autochthonous glauconitic clay of Whiteside and Robinson (1983) and ooids (Appendix 1). The ooids in samples U3, U4, but particularly in U6

(Appendix 2), indicate precipitation of calcium carbonate in swirling waters. We suggest that the ooids derive from $CaCO_3$-saturated meteoric waters flowing into similarly saturated marine waters in the cavern.

The relatively high proportions of gastropods (up to 6.28 % in sample U5; Appendix 4) with a preservation similar to that of BRSMG Cc479 (Fig. 10) in the cavern sediments indicates the presence of very shallow marine waters of the Westbury Formation near the entrance(s) to fissure 2 at Ex17 at the time of infilling. Numerous *Chemnitzia* specimens are visible in BRSMG Cc479, together with small, blackened bivalve-like steinkerns (Fig. 10B). Comparable specimens are relatively common in Ex17 samples (Appendix 4), although *Cylindrobullina* is only found in Cc479 (Fig. 10B). It is probable that the glauconitic rock region may have been the last cavity to form (by paragenesis) and fill, as the preceding fissure shape at 14 m suggests this part had not formed then (Figs. 2B, 3 A; Whiteside and Marshall, 2008).

We have constructed a model of the fissure 2 formation and infilling (Fig. 2A), developed from Whiteside and Marshall (2008). The fissure at Ex17 was filled by penecontemporaneous terrestrial and marine fossils and rock derived from the Carboniferous Limestone surface. The lower fissure fill consisted of initially fine silts and muds followed predominantly by conglomerates in the cavern. The clasts within the conglomerates include fossilised bones and rounded rocks which vary from unchanged Carboniferous Limestone to the metasomatically altered limestone suite observed in fissure 7 (Fig. 3G). Clasts with the same lithologies are found in the large-clast breccia of the *Thecodontosaurus* rock
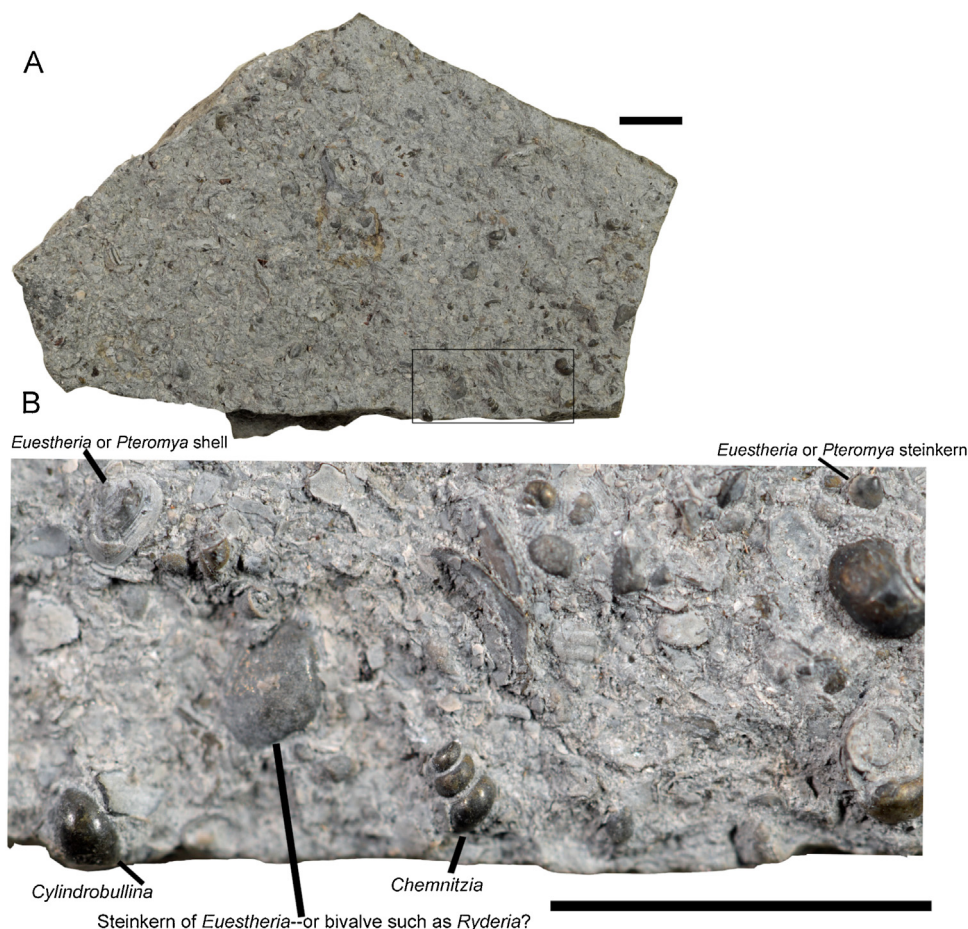
Fig. 10. Rock sample BRSMG Cc479 with typical lithology from the Westbury Formation of Patchway, Bristol showing numerous gastropods, bivalves and possibly some conchostracans. Scale bars = 1 cm.

(Whiteside and Marshall, 2008, figs. 7i, 8d) at Ex0. Breccia is uncommon in Ex17, only noticeable in samples U2 and U9 (also observable in Fig. 3E to the left of U9) and the large-clast dolomitic conglomerate of the exposure at 8 m (Fig. 3F) is absent.

Our new data strengthen the suggestion that fissure 2 was developed and infilled in a freshwater lens with the halocline (freshwater/seawater mixing zone) at Ex17. Passageways from the surface into the fissure, which lay about 20–30 m below the limestone surface, were widened by collapse of walls and rooves caused by dissolution and hydrodynamic action of meteoric waters. The hydrodynamic effects could be substantial, as shown by large pebbles of 'Dolomitic conglomerate'. In the exposures towards the north-west, the main fill input was breccias and conglomerates from a predominantly terrestrial source which included fossils of the fish *Pholidophorus* but mainly reptile bones of *Thecodontosaurus*, other archosaurs and sphenodontians. Further towards the south-east, the main fill comprised small-clast conglomerates and the same reptile fauna but with a greater marine component of *Gyrolepis*, other fishes, and gastropods. In or near the vicinity of the fissure entrance, possibly in more brackish waters, ostracods and conchostracans or bivalves inhabited the same waters as the gastropods. It is likely that the freshwater lens was dynamic, changing position seasonally, but our evidence suggests that the fissure 2 position at Ex17 was mainly developed and filled at the marine edge of this lens.

5.4. Dating of the fissure Ex17

The deposits of fissure 2 have been dated unequivocally as early Rhaetian by analysis of four palynomorph assemblages by Marshall and Whiteside (1980), Whiteside (1983), Whiteside and Marshall (2008) and Whiteside et al. (2016). The palynomorphs indicate a spread of time in the Westbury Formation equivalent to Beds 2–9 at Hampstead Farm Quarry (HFQ; Whiteside and Marshall, 2008; Whiteside et al., 2016). Whiteside and Marshall (2008) suggest that the gastropod steinkerns found in fissure 2 resemble those of the Westbury Formation (BRSMG Cc479; Fig. 10) from Patchway Bristol (although the specific horizon within the Westbury Formation is uncertain) and specimens from Bed 9 (top of the Westbury Formation) at HFQ depicted by Mears et al. (2016, fig. 17). The gastropods are facies-related fossils and probably do not convey detailed biostratigraphic information, but their presence, with other deeper water fauna absent, suggests a palaeoenvironment of shallow littoral waters. The nearest palynomorph sample to Ex17 was FP2.2 of Whiteside and Marshall (2008), who dated that assemblage as equivalent to the Lower Westbury beds 2 or 3 of HFQ.

There are no gastropods in the lower part of the fissure Ex17, but we have found abundant steinkerns preserved in typical Westbury Formation black phosphatic mineralogy throughout the cavern. Their highest proportions (U2 and U5) are in the lower part, but substantial numbers are found in almost all areas, including the glauconitic-clay rock, and there are high proportions in the upper part of the fissure at U8 and U9. The small crustacean steinkerns from four samples of the cavern are also preserved in typical Westbury lithology. *Gyrolepis*, a fish, is present in seven of 11 cavern samples and coeval fish fossils are found in nine of the 11, further confirming the close proximity of the marine Westbury Formation. Therefore, we conclude that cavern infilling occurred when the Westbury sea was adjacent to at least some of the fissure entrances. The palynomorph dating suggests, at its earliest, an age equivalent to the Lower Westbury Formation, or possibly later within the lower Rhaetian. The presence of all tetrapod genera in common to Ex17 and Ex0 suggests that the two exposures were penecontemporaneous. Recent dating of the clasts within the *Thecodontosaurus* breccia in Ex0 (Whiteside et al., 2016) as

equivalent to the lower or middle Westbury Formation at HFQ strengthens this suggestion. The bottom part of the fissure at Ex17 filled earlier, when the sea was further away (although it must still have been close for the cavern to have formed), but likely within a few thousand years of the upper fill.

6. Faunal sequence and associations

6.1. New findings

Determining whether differences in faunal composition within a single locality reflect taphonomic biases, ecological factors, or differences in the age of infilling has important implications for reconstructing the palaeoenvironment and biogeography of the Bristol fissures.

Since our study encompassed almost the entire stratigraphical sequence of a large fissure, we tested the samples for evidence of a faunal succession. With this in mind, a Kruskal-Wallis test was carried out to compare the relative abundance of major specimen types between the lower (L), upper (U), and glauconitic clay (G) sections of the exposure. Statistically significant differences ($p < 0.05$) between U and L, as well as G and L emerged for *Clevosaurus*, whereas the percentages of *Crossostoma* gastropods, reworked crinoid ossicles, and *Gyrolepis* teeth differed significantly between U and L (Appendix 5). Overall, significant percentage differences tend to emerge for Triassic marine taxa and for fossil types for which greater sample sizes are available, irrespective of whether they are reworked or not. In fact, a significant correlation ($p = 7.588e-06$) was found between the overall density of reworked and Triassic specimens across samples. These considerations suggest that in general, differences in the percentages of Triassic taxa within the stratigraphical sequence of the exposure reflect taphonomic phenomena, particularly in the selective transport of the fossils or increased marine influence, rather than biotic turnover.

In this regard, *Clevosaurus* and *Diphydontosaurus* are present in the lower and upper fissure of Ex17, but *Planocephalosaurus* is absent in the lower part and in the lowest samples of the cavern (L1–L5, the slump and U1). This indicates that, at least in this region, *Planocephalosaurus* was not present (or possibly very rare) in the vicinity of the entry fissures in the earliest sequence. Nor is *Planocephalosaurus* present in the samples with the highest marine component (U2 and U9), although it is consistently found in samples with a significant marine component (U4-U8, UDM, U11 and the glauconitic clay rock). *Clevosaurus* is the most abundant tetrapod and found in nearly all samples of the upper fill, but *Diphydontosaurus* is the most common in the lower fill and ubiquitous in the cavern. From our sampling, it seems reasonable to suggest that *Clevosaurus* and *Diphydontosaurus* inhabited the limestone surface at the margin of the littoral region of Tytherington island, but they were also found in more freshwater areas further inland.

To analyse faunal associations further we used a Fisher's exact test, in the manner of van den Berg et al. (2012), who found a statistically significant association between *Planocephalosaurus* and *Clevosaurus* fossils in their rock samples. This relationship could not be replicated in our study, but instead we found significant associations between *Clevosaurus* and *Diphydontosaurus* ($p = 0.01729$) and *Diphydontosaurus* and *Planocephalosaurus* ($p = 0.04455$). Although such differences might reflect a different sample size, and the first may simply be a consequence of the greater overall abundance of *Clevosaurus*, it is possible that they reflect real ecological phenomena. In particular, van den Berg et al. (2012) reported a relatively low co-occurrence of *Planocephalosaurus* and *Diphydontosaurus* and suggested ecological competition or different habitat preferences as a reason. However, it is

reasonable to consider that the niches of these two taxa may have increasingly overlapped as island size shrank during the Rhaetian as sea levels rose. In the case of the mid and upper cavern deposits the consistent marine influence suggests that the three sphenodontian genera were able to co-exist in the mosaic of freshwater/ brackish/ littoral habitats on the limestone surface above Ex17, but *Planocephalosaurus* disappears when increased saline conditions prevailed.

Other results of our analysis confirm some of the faunal associations described by van den Berg et al. (2012). In particular, a statistically significant association between archosaurs and *Clevosaurus* is upheld (p = 0.0436). Since *Clevosaurus* specimens and archosaur teeth differ greatly in size, shape, and robustness, this may reflect predator-prey relationships rather than taphonomic processes. Associations close to statistical significance are also found between archosaurs and the other sphenodontians. In addition, *Clevosaurus* and *Diphydontosaurus* associate significantly with reworked crinoid and/or chimaeroid material (Appendix 5). For *Clevosaurus*, a statistically significant (p = 0.03473) correlation with the percentage of reworked crinoids was also found. These results provide additional evidence that the sphenodontians lived on the exposed limestone surface and would have been washed into the fissures together with Carboniferous fossils (Whiteside and Marshall, 2008; van den Berg et al., 2012).

Uniquely among the Tytherington sphenodontians, *Clevosaurus* is found in statistically significant associations with the marine *Gyrolepis* and *Crossostoma* (Appendix 5). This finding strengthens suggestions that *Clevosaurus* may have thrived in littoral, heavily saline environments (Klein et al., 2015).

Moreover, a highly significant association (p = 0.005848) is found between *Thecodontosaurus* and *Terrestrisuchus*. Although the sample sizes for these taxa are too small to draw solid conclusions, it is worth noting that they represent the largest identified tetrapods from the exposure, and that their population sizes might have peaked at times of unusual biotic productivity or stability.

Finally, significant associations are detected between Triassic marine taxa, including *Crossostoma* and *Chemnitzia* (p = 0.04455) and *Crossostoma* and *Gyrolepis* (p = 0.01282). Although not significantly associated at the level of discrete rock samples, the percentages of *Gyrolepis* and *Chemnitzia* specimens show a highly significant positive correlation (p = 2.08e-05). The same holds true for *Crossostoma* and *Chemnitzia* (p = 0.003407). Taken together,

these results strongly suggest that the Triassic fishes and gastropods were coeval taxa, living in the neighbouring Rhaetian sea that may have intruded into low-lying limestone surface areas, and were frequently transported into the fissure together.

6.2. Comparison with other sampled exposures of fissure 2

The lack of evidence for major biotic turnover within the exposure and the signs of rapid (i.e. at most seasonal) variations in the mode of sedimentation, suggest that Ex17 of fissure 2 filled rapidly after its origin. Although all terrestrial tetrapod taxa (including the same species *D. avonis* and *P. robinsonae*) are common to both Ex17 and Ex0, the fossil faunas of the two sites differ in some important faunal proportions and variety of other taxa. Major differences in faunal percentages between the two exposures are shown in Fig. 11. As the procedures involved in our study and previous work (van den Berg et al., 2012) are nearly identical, these discrepancies cannot be easily explained by sieving or sampling biases.

The substantial differences between our results and those of van den Berg et al. (2012) indicate that individual exposures within the same fissure might record distinct periods of rapid infilling, in addition to localized habitat differences. However, as there are no major differences in tetrapod genera present/absent (e.g. many of the archosaur tooth morphotypes are in common) in Ex0 and Ex17, it is likely that the two exposures were penecontemporaneous but possibly not coeval.

Actinopterygian remains in Ex17 were found to be more abundant and taxonomically diverse than in the Ex0 described by van den Berg et al. (2012), with twice the number of identifiable tooth morphotypes in addition to scales and bony elements. In addition, marine and freshwater molluscs and crustaceans constitute a sizeable portion of the Triassic taxa of Ex17, representing almost 20 % of the total in the cavern. However, none of these invertebrates was reported from Ex0 by van den Berg et al. (2012), suggesting they may be considerably rarer or possibly absent in that section of the fissure. These findings confirm a greater marine influence at Ex17, as previously suggested by the presence of Triassic shark remains and glauconitic clay deposits (Whiteside, 1983; Whiteside and Marshall, 2008). Moreover, the black colour of the invertebrate steinkerns and some of the fish teeth from the upper section samples indicates fossilization in
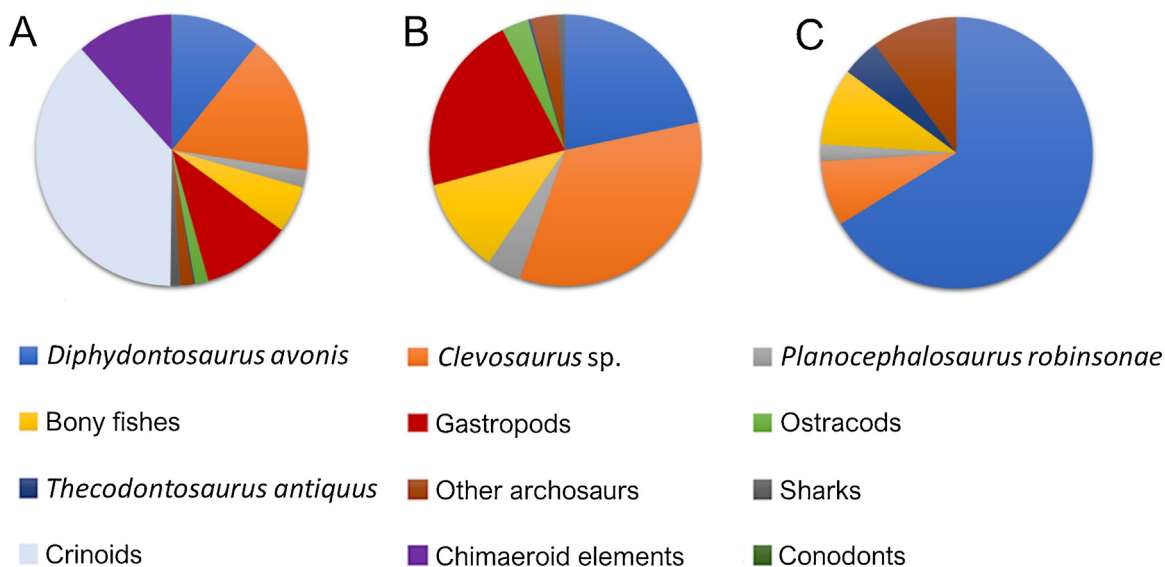
Fig. 11. Faunal composition of the Fissure 2 exposures, showing (A) all identifiable specimens from Ex17, including reworked taxa; (B) Identifiable Late Triassic specimens of Ex17; (C) Late Triassic specimens of Ex0, based on van den Berg et al. (2012).

anoxic conditions (Whiteside and Marshall, 2008), typical of the marine Westbury Formation. The brackish waters at the lime-stonesurface may have provided a suitable habitat for small bivalves or conchostracans and the *Darwinula*-type ostracods. Occasionally, these would have been washed into the saline waters nearby, where formation of the black sulphide steinkerns may have occurred. Saltwater gastropods may either have persisted in the saline layer or been washed into the fissure from the nearby sea. A littoral palaeoenvironment with a similar fauna was recorded associated with *Euestheria brodieana* by Richardson (1901) in the 'Estheria' bed (Cotham Member) of Gloucestershire. As previously discussed, the two-valved steinkerns from Ex17 may in fact be *Euestheria*.

Differences in terrestrial faunas are also worthy of interest. Previous studies identified *Diphydontosaurus avonis* as the most common Triassic sphenodontian in the eastern Tytherington fissures (Whiteside and Marshall, 2008, fig. 17), especially Fissure 2 (van den Berg et al., 2012, fig. 6). At Ex0 of Fissure 2, this taxon represents more than two-thirds of all non-reworked specimens (van den Berg et al., 2012, fig. 6B). In contrast, although *Diphydontosaurus* occurs in more samples in total than *Clevosaurus* in Ex17, the Late Triassic assemblages of Ex17 are numerically dominated by *Clevosaurus*, which represents almost 30 % of non-reworked taxa, whereas *Diphydontosaurus* comprises less than 20 %. As previously discussed, the abundance of *Clevosaurus* might partially reflect taphonomic biases. However, the percentages of sphenodontians in Ex17 are line with the NW-SE cline described by Klein et al. (2015), wherein *Clevosaurus* becomes almost the only terrestrial taxon in Woodleaze, 800 m to the SE. Overall, sphenodontian faunas from the marginal marine Ex17 of Tytherington Fissure 2 also show greater species evenness than those of Tytherington Ex0.

Archosaurs were found to be considerably less abundant in Ex17, representing only about 2.7 % of identified Triassic specimens (1.4 % if reworked taxa are included). On the other hand, van den Berg et al. (2012) reported that archosaurs represented 6–8 % of the identifiable material in Ex0. In particular, *Thecodontosaurus* is much rarer in Ex17, where it is represented by three fragments (i.e. about 0.2 % of the identified Triassic specimens). In the faunas of Ex0, *Thecodontosaurus* remains comprise minimally 2–3 % of all material (van den Berg et al., 2012). However, it is interesting that both *Thecodontosaurus* and *Terrestrisuchus* are found in U8, in close proximity to the brecciated rocks of U9; they are found also in the breccias of Ex0.

It may seem unlikely that the relative abundance of taxa is significantly different between two exposures 17 m apart, but this could reflect a greater seawater input on the limestone surface at Ex17, which is strongly indicated by our faunal analysis. In particular, the greater abundance of *Clevosaurus* may be explained by a preference of this taxon for saline coastal habitats, as suggested by Klein et al. (2015) and our analysis of faunal associations. The herbivorous larger animals, such as *Thecodonto-saurus*, which shows a much greater abundance at Ex0, are likely to have preferred the more diverse and lush vegetation in the freshwater areas above that part of the fissure. Similarly, the larger carnivorous archosaurs may have been associated with more productive habitats further inland. Other differences in propor-tions of the fauna at Ex0 and Ex17 probably relate to differential transport of bones and teeth; the fact that much larger clasts predominate in the breccias and conglomerates towards the NW of fissure 2, and particularly at Ex0, is in accord with this suggestion.

6.3. Comparison with other Tytherington fissures

Discrepancies in faunal composition between different fissures at Tytherington (Whiteside and Marshall, 2008) and Cromhall (Fraser and Walkden, 1983) may reflect ecological differences

across microhabitats (Whiteside and Marshall, 2008) rather than just different times of deposition.

In our study of 17 rock samples through a single fissure, we found no evidence of the sphenodontians *Pelecymala*, *Sigmala* and the procolophonid (termed '*Tricuspisaurus*' by Whiteside and Marshall, 2008) which are found in fissure 14. Nor is there any fossil that could be the 'lepidosaur B' of Whiteside and Marshall (2008) which is unique to fissure 12. These findings suggest that the faunal assemblage of fissure 2 is distinct from fissures 12 and 14. Further, gastropods and *Gyrolepis* are recorded from fissure 14 by Whiteside and Marshall (2008), but occur in far smaller proportions (only one *Gyrolepis* tooth was found) than in fissure 2, so that assemblage is almost entirely terrestrial. It remains unresolved whether the faunal contrast between fissures 2 and 14 reflects partitioning of coeval local niches on the limestone surface or different times of deposition. The latter is perhaps more likely as it more plausibly explains the absence of *Pelecymala*, *Sigmala* and a procolophonid in fissure 2 whereas fissure 14 lacks *Thecodontosaurus*.

6.4. Comparisons with other nearby fissure localities

The mapping of fossil taxa across the depth of Fissure 2 allows comparisons to be made with other Bristol fissure sites, including Durdham Down (Foffa et al., 2014) Cromhall Quarry (Fraser and Walkden, 1983, 1993; Fraser, 1985, 1988b) and Woodleaze Quarry (Klein et al., 2015). Our analysis of Ex17 in fissure 2 demonstrates that there is little biotic turnover over 6 m of vertical fill except for an increasing influx of coeval marine fauna. This therefore contradicts the suggestions made by Fraser (1985) for this fissure that a later marine fauna was added to earlier continental deposits ('redistribution' of Fraser, 1985) or Walkden and Fraser's (1993) comment that fissure 2 includes mixed faunas from different time periods through repeated avalanching of accumulated sediment. Rather, despite examples of cavern collapse (particularly in Ex0) the deposits of fissure 2 formed from terrestrial and aquatic faunas that are washed in together and form a sequence that probably represents only a few thousand years at most.

The evidence for a Rhaetian age of solution and infilling of the Tytherington fissures, and of other Late Triassic fissure localities across the SW UK, has been extensively discussed elsewhere (Marshall and Whiteside, 1980; Whiteside, 1983; Whiteside and Marshall, 2008; van den Berg et al., 2012; Foffa et al., 2014; Klein et al., 2015; Nordén et al., 2015; Whiteside et al., 2016). The Durdham Down (Foffa et al., 2014), Cromhall (Whiteside et al., 2016) and Woodleaze (Klein et al., 2015) faunas all have coeval marine fossils, giving consistent evidence of a marine transgression event, which is best explained by a Rhaetian infilling. The locations Ex17 and Ex0 of Tytherington fissure 2 provide the best evidence of this.

Faunal associations across different fissure localities also show some consistent patterns. *Clevosaurus* tends to dominate sphenodontian assemblages in more heavily marine deposits with depauperate terrestrial faunas. This trend emerges between different fissures at Cromhall (Walkden and Fraser, 1993), in the comparison between Ex0 and Ex17 at Tytherington, and culmi-nates in the heavily saline, almost monofaunal Woodleaze deposit described by Klein et al. (2015). Moreover, it is in line with the associations between *Clevosaurus* and marine taxa (Appendix 5), its inferred generalist ecology (Fraser, 1985) and its probable persistence into the Lower Jurassic, at a time of reduced island size and greater marine influence following the Rhaetian Transgression (Säilä, 2005; Whiteside et al., 2016). Conversely, *Planocephalosau-rus* is absent from the more marine samples of Ex17, and from fissures with a significant marine influence at Cromhall (Walkden and Fraser, 1993). As previously discussed, this could be partly explained by geographical differences, or reflect environmental change during different phases of the Rhaetian Transgression.

Drastic changes in insular ecosystems as a result of sea level changes are known to occur over intervals in the order of thousands of years, as in Aldabra (Taylor et al., 1979; Hume et al., 2018) and the Bahamas (Steadman et al., 2015) during the Pleistocene. It is likely that the faunal sequences of individual Tytherington and Cromhall fissure fills span a similar timeframe, within the duration of the Rhaetian Transgression. The possibility that each fissure site may reflect similar responses to separate transgression events extending to pre-Rhaetian times is unlikely, as there is no faunal or geomorphological evidence of a pre-Rhaetian fissure filling. However, the possibility that distinct fissure sites may record separate transgression pulses during the Rhaetian (e.g. Hamilton, 1962) cannot be excluded.

7. Future work and conclusion

Establishing a specific temporal correspondence between the Cromhall, Durdham Down, Tytherington, and Woodleaze Late Triassic faunas may not be possible, in the face of confounding effects of local environmental variations and multiple Rhaetian transgression pulses. Nonetheless, we have found no evidence of any taxa that have been considered pre-Rhaetian by other authors (e.g. Fraser and Walkden, 1983). In fact, there is increasing evidence that the sauropsid fissures are equivalent in age to the Penarth Group marine units, and fissure 2 demonstrates faunal, lithological and geomorphological consistency with the lower Rhaetian Westbury Formation. Similar evidence places Durdham Down, Woodleaze and some fissures in Cromhall within the Westbury Formation. Furthermore, there is now additional biostratigraphic evidence from the presence of *Euestheria brodieana* that sediments that contain *Clevosaurus hudsoni* at Cromhall are equivalent to the upper Rhaetian Cotham Member of the Lilstock Formation (Morton et al., 2017). Ideally, the response of Rhaetian insular taxa to rising sea levels could be tested by extending systematic faunal comparisons across individual fissures of a single site, or even multiple exposures of a single fissure. However, modern health and safety regulations mean it is unlikely that the systematic sampling of a fissure exposure in a working quarry face could be attempted today, highlighting the uniqueness of the analysis that we have been able to undertake.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pgeola.2019.12.001.

References

Agassiz, J.L.R., 1833–1843 Recherches sur les poissons fossiles. Tome 3, concernant l'histoire de l'ordre des placoïdes. Imprimerie Petitpierre, Neuchâtel 390 + 34 pp.

Allard, H., Carpenter, S., Duffin, C.J., Benton, M.J., 2015. Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK). Proceedings of the Geologists' Association 126, 762–776.

Benton, M.J., 1995. Diversification and extinction in the history of life. Science 268, 52–58.

Benton, M.J., Juul, L., Storrs, G.W., Galton, P.M., 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of Southwest England. Journal of Vertebrate Paleontology 20, 77–108.

Benton, M.J., Schouten, R., Drewitt, E.J.A., Viegas, P., 2012. The Bristol Dinosaur Project. Proceedings of the Geologists' Association 123, 210–222.

Benton, M.J., Spencer, P.S., 1995. Fossil Reptiles of Great Britain. Chapman and Hall, London 386 pp.

Benton, M.J., Forth, J., Langer, M.C., 2014. Models for the rise of the dinosaurs. Current Biology 24, R87–R95.

Buckley, L.G., Currie, P.J., 2014. Analysis of intraspecific and ontogenetic variation in the dentition of *Coelophysis bauri* (Late Triassic), and implications for the systematics of isolated theropod teeth. New Mexico Museum of Natural History and Science, Bulletin 63, 1–73.

Cross, S.R., Ivanovski, N., Duffin, C.J., Hildebrandt, C., Parker, A., Benton, M.J., 2018. Microvertebrates from the basal Rhaetian Bone Bed (latest Triassic) at Aust Cliff, SW England. Proceedings of the Geologists' Association 129, 635–653.

Crush, P.J., 1984. A late Upper Triassic sphenosuchid crocodilian from Wales. Palaeontology 27, 131–157.

Cuny, G., Benton, M.J., 1999. Early radiation of the neoselachian sharks in Western Europe. Geobios 32, 193–204.

Deenen, M.H.L., Ruhl, M., Bonis, N.R., Krijgsman, W., Kuerschner, W., Reitsma, M., vanBergen, M.J., 2010. A new chronology for the end-Triassic mass extinction. Earth and Planetary Science Letters 291, 113–125.

d'Orbigny, A., 1850. Prodrome de Paléontologie Stratigraphique Universelle des Animaux Mollusques et Rayonnés, vol. 1. Masson, Paris 394 pp.

Duffin, C.J., 1993. New record of the phoebodontid chondrichthyan *Thrinacodus ferox* (Turner, 1982) from the Carboniferous of England. In: Herman, J., Van Waes, H. (Eds.), Elasmobranches et Stratigraphie. Belgian Geological Survey, Professional Paper 264, , pp. 1–6.

Dunhill, A.M., Foster, W.J., Sciberras, J., Twitchett, R.J., 2018. Impact of the Late Triassic mass extinction on functional diversity and composition of marine ecosystems. Palaeontology 61, 133–148.

Farrant, A.R., Smart, P.L., 2011. Role of sediment in speleogenesis; sedimentation and paragenesis. Geomorphology 134, 79–93.

Fischer, J., Voigt, S., Franz, M., Schneider, J.W., Joachimski, M.M., Tichomirowa, M., Götze, J., Furrer, H., 2012. Palaeoenvironments of the late Triassic Rhaetian Sea: implications from oxygen and strontium isotopes of hybodont shark teeth. Palaeogeography, Palaeoclimatology, Palaeoecology 353–355, 60–72.

Foffa, D., Whiteside, D.I., Viegas, P.A., Benton, M.J., 2014. Vertebrates from the Late Triassic *Thecodontosaurus*-bearing rocks of Durdham Down, Clifton (Bristol, UK). Proceedings of the Geologists' Association 125, 317–328.

Fraser, N.C., 1982. A new rhynchocephalian from the British Upper Trias. Palaeontology 25, 709–725.

Fraser, N.C., 1985. Vertebrate faunas from Mesozoic fissure deposits of South West Britain. Modern Geology 9, 273–300.

Fraser, N.C., 1986. New Triassic sphenodontids from south-west England and a review of their classification. Palaeontology 29, 165–186.

Fraser, N.C., 1988a. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Philosophical Transactions of the Royal Society of London B 321, 125–178.

Fraser, N.C., 1988b. Latest Triassic terrestrial vertebrates and their biostratigraphy. Modern Geology 13, 125–140.

Fraser, N.C., 1994. Assemblages of small tetrapods from British Late Triassic fissure deposits. In: Fraser, N.C., Sues, H.-D. (Eds.), In the Shadow of the Dinosaurs. Cambridge University Press, New York, pp. 214–226.

Fraser, N.C., Walkden, G.M., 1983. The ecology of a Late Triassic reptile assemblage from Gloucestershire, England. Palaeogeography, Palaeoclimatology, Palaeoecology 42, 341–365.

Fraser, N.C., Walkden, G.M., 1984. Postcranial skeleton of the Upper Triassic sphenodontid *Planocephalosaurus robinsonae*. Palaeontology 27, 575–595.

Friedman, M., Sallan, L.C., 2012. Five hundred million years of extinction and recovery: a phanerozoic survey of large-scale diversity patterns in fishes. Palaeontology 55, 707–742.

Ginter, M., Duffin, C.J., Dean, M.T., Korn, D., 2015. Late Viséan pelagic chondrichthyans from northern Europe. Acta Palaeontologica Polonica 60, 899–922.

Ginter, M., Turner, S., 2010. The middle Paleozoic selachian genus *Thrinacodus*. Journal of Vertebrate Paleontology 30, 1666–1672.

Godefroit, P., Knoll, F., 2003. Late Triassic dinosaur teeth from southern Belgium. Comptes Rendus Palevol 2, 3–11.

Guinot, G., Adnet, S., Cappetta, H., 2012. An analytical approach for estimating fossil record and diversification events in sharks, skates and rays. PLoS One 7 (9), 44632.

Hallam, A., 2002. How catastrophic was the end-Triassic mass extinction? Lethaia 35, 147–157.

Hamilton, D., 1962. Some notes on the Rhaetic sediments of the Filton by-pass substitute, near Bristol. Proceedings of the Bristol Naturalists' Society 30, 279–285.

Heckert, A.B., 2004. The Late Triassic microvertebrates from the Lower Chinle Group (Otischalkian-Adamanian: Carnian), southwestern USA. New Mexico Museum of Natural History and Science, Bulletin 27, 1–170.

Hume, J.P., Martill, D., Hing, R., 2018. A terrestrial vertebrate palaeontological review of Aldabra Atoll, Aldabra Group, Seychelles. PLoS One 13 (3), e0192675.

Keeble, E., Whiteside, D.I., Benton, M.J., 2018. The terrestrial fauna of the Late Triassic Pant-y-ffynnon Quarry fissures, South Wales, UK and a new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia). Proceedings of the Geologists' Association 129, 99–119.

Kent, D.V., Olsen, P.E., Muttoni, G., 2017. Astrochronostratigraphic polarity time scale (APTS) for the Late Triassic and Early Jurassic from continental sediments and correlation with standard marine stages. Earth-Science Reviews 166, 153–180.

Klein, C.G., Whiteside, D.I., Selles de Lucas, V., Viegas, P.A., Benton, M.J., 2015. A distinctive Late Triassic microvertebrate fissure fauna and a new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from Woodleaze Quarry, Gloucestershire, UK. Proceedings of the Geologists' Association 126, 402–416.

Lakin, R.J., Duffin, C.J., Hildebrandt, C., Benton, M.J., 2016. The Rhaetian vertebrates of Chipping Sodbury, South Gloucestershire, UK, a comparative study. Proceedings of the Geologists' Association 127, 40–52.

Landon, E.N.U., Duffin, C.J., Hildebrandt, C., Davies, T.G., Simms, M.J., Benton, M.J., 2017. The first discovery of crinoids and cephalopod hooklets in the British Triassic. Proceedings of the Geologists' Association 128, 360–373.

Maisey, J.G., 1981. Studies on the Paleozoic selachian genus *Ctenacanthus* Agassiz. No. 1, Historical review and revised diagnosis *of Ctenacanthus*, with a list of referred taxa. American Museum Novitates 2718, 1–22.

Maisey, J.G., 1986. Anatomical revision of the fossil shark *Hybodus fraasi* (Chondrichthyes: Elasmobranchii). American Museum Novitates 2857, 1–16.

Marshall, J.E.A., Whiteside, D.I., 1980. Marine influence in the Triassic 'uplands'. Nature 287, 627–628.

Mears, E., Rossi, V., MacDonald, E., Coleman, G., Davies, T.G., Riesgo, C., Hildebrandt, C., Thiel, H., Duffin, C.J., Whiteside, D.I., Benton, M.J., 2016. The Rhaetian vertebrates of Hampstead Farm Quarry, Gloucestershire, UK. Proceedings of the Geologist's Association 127, 478–505.

Moore, C., 1867. On abnormal conditions of Secondary deposits when connected with the Somersetshire and South Wales Coal-Basin; and on the age of the Sutton and Southerndown Series. Quarterly Journal of the Geological Society 23, 449–568.

Morris, J., 1843. A Catalogue of British Fossils. J. van Voorst, London 222 pp.

Morton, J.D., Whiteside, D.I., Hethke, M., Benton, M.J., 2017. Biostratigraphy and geometric morphometrics of conchostracans (Crustacea, Branchiopoda) from the Late Triassic fissure deposits of Cromhall Quarry, UK. Palaeontology 60, 349–374.

Mutt, R.J., Rieber, H., 2005. *Pyknotylacanthus spathianus* gen. et sp. nov., a new ctenacanthid from the Early Triassic of Bear Lake (Idaho, USA). Revista Brasileira de Paleontologia 8, 139–148.

Mylroie, J.E., Mylroie, J.R., 2007. Development of the carbonate island karst model. Journal of Cave and Karst Studies 69, 59–75.

Mylroie, J.E., Mylroie, J.R., 2013. Caves and karst of the Bahama Islands. In: Lace, M.J., Mylroie, J.E. (Eds.), Coastal Karst Landforms. Springer, Dordrecht, pp. 147–176.

Nesbitt, S., Desojo, J., Irmis, R.B., 2013. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geological Society of London Special Publications, London 608 pp.

Nordén, K., Duffin, C.J., Benton, M.J., 2015. A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. Proceedings of the Geologists' Association 126, 564–581.

Parker, W.G., Irmis, R.B., Nesbitt, S.J., Martz, J.W., Browne, L.S., 2005. The late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. Proceedings of the Royal Society B 272, 963–969.

Percival, L.M., Ruhl, M., Hesselbo, S.P., Jenkyns, H.C., Mather, T.A., Whiteside, J.H., 2017. Mercury evidence for pulsed volcanism during the end-Triassic mass extinction. Proceedings of the National Academy of Sciences, U.S.A. 114, 7929–7934.

Richardson, L., 1901. On the *Estheria*-bed in north-west Gloucestershire and the organic associations of *Estheria minuta* var. *brodieana*. Proceedings of the Bristol Naturalists (new series) 10, 72–76.

Robinson, P.L., 1957. The Mesozoic fissures of the Bristol Channel area and their vertebrate faunas. Journal of the Linnean Society of London, Zoology 43, 260–282.

Robinson, P.L., 1973. A problematic reptile from the British Upper Trias. Journal of the Geological Society, London 129, 457–479.

Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., Bucher, H., Kriwet, J., 2014. Permian-Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. Biological Reviews 91, 106–147.

Säilä, L.K., 2005. A new species of the sphenodontian reptile *Clevosaurus* from the Lower Jurassic of South Wales. Palaeontology 48, 817–831.

Savage, R.J.G., 1993. Vertebrate fissure faunas with special reference to Bristol Channel Mesozoic faunas. Journal of the Geological Society, London 150, 1025–1034.

Schoene, B., Guex, J., Bartolini, A., Schaltegger, U., Blackburn, T.J., 2010. A correlation between the Triassic–Jurassic boundary mass extinction and flood basalt eruption at the 100 ka-level using ID-TIMS U/Pb zircon geochronology. Geology 38, 387–390.

Simms, M.J., Ruffell, A.H., Johnston, A.L.A., 1994. Biotic and climatic changes in the Carnian (Triassic) of Europe and adjacent areas. In: Fraser, N.C., Sues, H.-D. (Eds.), In the Shadow of the Dinosaurs. Cambridge University Press, New York, pp. 352–365.

Singurindy, O., Berkowitz, B., Lowell, R.P., 2004. Carbonate dissolution and precipitation in coastal environments: laboratory analysis and theoretical consideration. Water Resources Research 40, W04401.

Smart, P.L., Dawans, J.M., Whitaker, F., 1988. Carbonate dissolution in a modern mixing zone. Nature 335, 811–813.

Smithwick, F.M., Stubbs, T.L., 2018. Phanerozoic survivors: actinopterygian evolution through the Permo-Triassic and Triassic-Jurassic mass extinction events. Evolution 72, 348–362.

Steadman, D.W., Albury, N.A., Kakuk, B., Mead, J.I., Soto-Centeno, J.A., Singleton, H. M., Franklin, J., 2015. Vertebrate community on an ice-age Caribbean island. Proceedings of the National Academy of Sciences, U.S.A. 112, E5963–E5971.

Storrs, G.W., 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). Zoological Journal of the Linnean Society 112, 217–259.

Suan, G., Föllmi, K.B., Adatte, T., Bomou, B., Spangenberg, J.E., van de Schootbrugge, B., 2012. Major environmental change and bonebed genesis prior to the Triassic–Jurassic mass extinction. Journal of the Geological Society 169, 191–200.

Sues, H.-D., Fraser, N.C., 2010. Triassic Life on Land. Columbia University Press, New York 280 pp.

Swift, A., Martill, D.M., 1999. Fossils of the Rhaetian Penarth Group. Field Guides to Fossils 9. Palaeontological Association, London 312 pp.

Tanner, L.H. (Ed.), 2018. The Late Triassic World: Earth in a Time of Transition. Springer, New York 805 pp.

Tanner, L.H., Lucas, S.G., Chapman, M.G., 2004. Assessing the record and causes of Late Triassic extinctions. Earth-Science Reviews 65, 103–139.

Taylor, J.D., Braithwaite, C.J.R., Peake, J.F., Arnold, E.N., 1979. Terrestrial faunas and habitats of Aldabra during the late Pleistocene. Philosophical Transactions of the Royal Society B 286, 47–66.

Thorne, P.M., Ruta, M., Benton, M.J., 2011. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. Proceedings of the National Academy of Sciences, U.S.A. 108, 8339–8344.

Turner, S., 1982. Middle Palaeozoic elasmobranch remains from Australia. Journal of Vertebrate Paleontology 2, 117–131.

van den Berg, T., Whiteside, D.I., Viegas, P., Schouten, R., Benton, M.J., 2012. The Late Triassic microvertebrate fauna of Tytherington, UK. Proceedings of the Geologists' Association 123, 638–648.

Walkden, G.M., Fraser, N.C., 1993. Late Triassic fissure sediments and vertebrate faunas: Environmental change and faunal succession at Cromhall, South West Britain. Modern Geology 18, 511–535.

Whitaker, F.F., Smart, P.L., 2007. Geochemistry of meteoric diagenesis in carbonate islands of the northern Bahamas: 1. Evidence from field studies. Hydrological Processes 21, 949–966.

Whiteside, D.I., 1983. A fissure fauna from Avon. Unpublished Ph.D. Thesis. University of Bristol.

Whiteside, D.I., 1986. The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et. sp. nov. and the modernizing of a living fossil. Philosophical Transactions of the Royal Society B 312, 379–430.

Whiteside, D.I., Duffin, C.J., Gill, P.G., Marshall, J.E.A., Benton, M.J., 2016. The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: stratigraphy and setting. Palaeontologia Polonica 67, 257–287.

Whiteside, D.I., Marshall, J.E.A., 2008. The age, fauna and palaeoenvironment of the late Triassic fissure deposits of Tytherington, South Gloucestershire, UK. Geological Magazine 145, 105–147.

Whiteside, D.I., Robinson, D., 1983. A glauconitic clay–mineral from a speleological deposit of Late Triassic age. Palaeogeography, Palaeoclimatology, Palaeoecology 41, 81–85.